BRITISH WEALDEN SHARKS

BY

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SYNOPSIS

New material, consisting mainly of abundant isolated teeth from bone-beds, allows more detailed and precise definition of the known sharks of the British Wealden and Purbeck, and contains five new species : *Hybodus brevicostatus*, *Lonchidion breve* (with three new subspecies), *L. striatum*, *L. rhizion* and *L. heterodon*. Samples from successive horizons allow the interrelationships of the various species to be worked out in some detail. *Hylaeobatis* is shown to belong in the family Ptychodontidae and to lie near the ancestry of *Ptychodus* : the Ptychodontidae are probably derived from the hybodontid genus *Lonchidion*. The Wealden shark fauna is unusual in being from fresh water and in containing only hybodontoids : it is suggested that the hybodonts were able to escape from competition with more advanced selachians by entering fresh water : the radiation which they underwent there parallels their marine radiation at their first appearance, and explains the similarity between the shark fauna of the Wealden and of the marine Triassic. Certain of the more specialized Wealden forms seem to have returned to the sea and given rise to the Upper Cretaceous hybodonts and ptychodonts.

I INTRODUCTION

This paper has been prompted by the arrival in the British Museum (Natural History) of two sets of new Wealden material. Between 1960 and 1962 Drs. W. A. Clemens and K. A. Kermack of University College, London, were searching the bone-beds of the British Wealden for mammalian remains. In the course of this work large quantities of bone-bed were broken down with formic acid, and the bone separated by bromoform flotation. The mammalian finds resulting from the work have already been described (Clemens 1960, 1963; Kermack, Lees & Mussett 1965), and Dr. Kermack and his colleagues were kind enough to present the residue of the treated bone-beds to this museum. This material is rich in fish remains, though the majority are rolled and water-worn. In 1961 Mr. J. F. Wyley of Richmond, Surrey, discovered a bone-bed in the Weald Clay in the Henfield Brick Company's pit at Henfield, Sussex, and in many visits to the pit he has collected a quantity of fish material which he has generously presented to this museum. The material from Henfield is normally excellently preserved.

Knowledge of British Wealden sharks is due almost entirely to Smith Woodward. Agassiz (1837) described several hybodont fin spines under various names, and Egerton (1845) described *Hybodus basanus* from the Weald Clay of the Isle of Wight and (1854) a fin spine from Tilgate as *Asteracanthus granulosus*. In 1889 Smith Woodward briefly redescribed these species, referred several teeth to *Hybodus*, and described *Acrodus ornatus* from the Upper Wealden. Later (Smith Woodward 1916), in his monograph on the fishes of the British Wealden and Purbeck, he gave more detailed descriptions of all these species and added two new species of *Hybodus*, *H. ensis* and *H. parvidens*, and a new genus and species, *Hylaeobatis problematica*, all based on isolated teeth. No new material of any of these species has since been described (*H. basanus* has been incorrectly recorded from the Cretaceous of Japan by Yabe & Obata 1930).

In this paper a new species of *Hybodus* and four new species, one with three subspecies, of the hybodont genus *Lonchidion* Estes (1964) are described, and *Acrodus ornatus* and *Hylaeobatis problematica* are shown to be synonymous. The total list of British Wealden sharks known at present is therefore :

Hybodus basanus Egerton
**H. ensis* Smith Woodward
**H. parvidens* Smith Woodward
H. brevicostatus sp. nov.
†*H. striatulus* Agassiz
**Lonchidion breve* sp. nov.
**L. striatum* sp. nov.
**L. rhizion* sp. nov.
**L. heterodon* sp. nov.
†*Asteracanthus granulosus* Egerton (doubtfully *Asteracanthus*, see p. 310)
**Hylaeobatis ornata* (Smith Woodward)

* Species known only by isolated teeth.
† Species known only by isolated fin spines.

II LOCALITIES

The bulk of the new material described here is from four horizons, the Cliff End bone-bed, the Telham bone-bed, the Paddockhurst bone-bed and the Weald Clay of Henfield, Sussex.

(*a*) Cliff End Bone-bed

The Cliff End bone-bed, exposed on the foreshore at Cliff End, near Hastings, Sussex, the source of the mammal teeth discovered early in the century by Teilhard de Chardin and Pelletier, has recently been described by Allen (1960 : 11) and Clemens (1963 : 58), the latter also describing the method used to concentrate the vertebrate remains. The bone-bed is within the Ashdown Beds (of Valanginian age according to Hughes 1958), but its precise horizon is not yet established*. The Ashdown Beds are interpreted by Allen (1959) as a deltaic deposit, the delta flowing into a fresh-water lake. The great majority of the vertebrate remains are strongly rolled and abraded. Of the recognizable fragments about 45% are shark teeth, 50% are teeth and fragments of dermal bones of actinopterygians (mainly *Lepidotes*), and 5% or less are reptilian.

The shark fauna includes :

Hybodus ensis (common)
H. parvidens (common)
H. brevicostatus (rare)
Lonchidion breve breve (moderately common)
L. rhizion (uncommon)
L. heterodon (rare)

(*b*) Telham Bone-bed

The Telham bone-bed is exposed at a number of localities in the south-eastern Weald (Allen 1949 : 279, text-fig. 45). The sample described here was collected by Mr. P. J. Whybrow from the exposure at Teigh Farm, Stone, Kent (GR TQ 937268). The bone-bed lies in the Wadhurst Clay, near the base (Upper Valanginian according to Hughes 1958), and is interpreted by Allen as the result of river water flooding over a delta plain. The vertebrate remains are in much the same condition as at Cliff End, rolled and abraded. Of the recognizable fragments, about 30% are shark teeth and the remaining 70% are almost entirely actinopterygian, mainly *Lepidotes* : reptiles account for only about 1% of the sample. The shark fauna includes :

Hybodus ensis (rare)
H. parvidens (common)
Lonchidion breve breve (moderately common)
L. rhizion (rare)

This locality is referred to in the text as Telham bone-bed, Stone, Kent.

* In a paper published while this work was in press, Kermack, Lees & Mussett (1965: 536) give further information on the Cliff End bone-bed, pointing out that the bed cannot now be located in the cliff or on the foreshore, and that the scattered blocks found on the beach probably come from an off-shore reef, which would place the bone-bed "well down in the Fairlight Clays", near the base of the Wealden. Kermack, Lees & Mussett also publish a comment on the Cliff End fauna which I wrote on first seeing the material. I would not now infer brackish conditions from the abundant hybodont selachians: I think it probable that all the species present were capable of life in fresh water.

(*c*) Paddockhurst Bone-bed

Clemens (1960, 1963 : 63) has given this name to a bone-bed in the Grinstead Clay (Hauterivian according to Hughes 1958) at Paddockhurst Park, near Turner's Hill, Sussex. Allen (1959) interprets the Grinstead Clay as a fresh-water lake deposit. The vertebrate remains in the Paddockhurst bone-bed are neither so broken up nor so badly rolled as they are at Cliff End, and sharks are less common : shark teeth make up about 15% of the recognizable elements, reptiles about 10%, and the remaining 75% is actinopterygian, mainly scales and teeth of *Lepidotes*.

The shark fauna includes :

Hybodus ensis (common)
H. parvidens (common)
H. brevicostatus (rare)
Lonchidion breve breve (moderately common)
L. breve crenulatum (moderately common)
L. rhizion (rare)

(*d*) Henfield

The Henfield Brick Company's pit (GR TQ/218143) at Henfield, Sussex, is a large pit in the Weald Clay which is being actively worked (Milbourne 1961 : 135). The beds dip northwards at about 5 degrees (Reeves 1947 : 83). The highest beds exposed, in the north wall of the pit, are red and yellow clays without obvious fossils. These beds pass down into brown and grey clays. About 3 ft. below the red and yellow clays there is a band of '*Paludina*' limestone, 3–8 in. thick. Fishes occur in the clay immediately above the limestone. Below the limestone there is 10 ft. of brown sandy clay, and below this about 25 ft. of grey clay in which six minor cyclothems, 3–4 ft. thick, are recognizable by increasing sand content giving a brownish tinge towards the top of each. Each of these cyclothems contains fish fragments, often concentrated into more or less well marked bone-beds which are occasionally cemented into a phosphatic limestone (Pl. 1, fig. 1). Below these cyclothems the floor of the pit is occupied by grey clay containing *Iguanodon*, lignite and occasional tree trunks, passing down in the south wall of the pit into barren red and yellow clays and sands, the lowest beds exposed. This sequence lies in Reeve's Group II (1958 : 11), the middle division of the Weald Clay (Barremian according to Allen 1955 and Hughes 1958), probably near the top : Dr. F. W. Anderson has examined samples of ostracods collected from the various fish horizons and places the '*Paludina*' limestone at about 550 ft. below the top of the Weald Clay.

Associated with the fishes there are abundant ostracods, all non-marine according to Dr. Anderson, and occasional charophyte oogonia, another indication of fresh water conditions. The fish material, although consisting almost entirely of dissociated fragments, is well preserved. There is no significant difference in the fish fauna of the various fish horizons, but in the minor cyclothems the fauna varies widely within the bone-beds: the block of bone-bed shown in Pl. 1, fig. 1 shows abundant shark teeth of five species (teeth of *Lonchidion breve* and *L. striatum* are too small to show on the photograph), but the other side of the block, which is only 14 mm.

thick, shows only two or three teeth of *Lonchidion*, and is made up almost entirely of teleostean remains. Sharks make up less than 10% of the material, the bulk of which is teleostean. Actinopterygians identified include:

Lepidotes mantelli Agassiz
Coelodus mantelli Agassiz
Caturus tenuidens Smith Woodward (Pl. 1, fig. 2: not previously recorded above the Purbeck)
Pachythrissops sp.
Clupavus sp.

The shark fauna includes:

Hybodus basanus (common)
H. parvidens (rare)
H. brevicostatus (moderately common)
Lonchidion breve breve (common)
Lonchidion striatum (common)
Hylaeobatis ornata (common)

(*e*) Other localities

Small but valuable samples from two other localities are also described here. The first was collected by Mr. I. M. West of the University of Southampton from a limestone above the Broken Shell Limestone in the Upper Purbeck exposed 100 yards east of Friar Waddon farm, near Upwey, Dorset (GR SY/643858) (see Anderson 1958: 119, 129, text-figs. 21, 22). Mr. West thinks this horizon is equivalent to the *Unio* Bed of the type Purbeck. The second sample was collected by Mr. P. J. Whybrow from a limestone in the Wadhurst Clay exposed in a cutting on the east side of the road 200 yards north of Homeland, Ashurstwood, Sussex (GR TQ/419363). These two localities are referred to in the text as Friar Waddon and Ashurstwood respectively.

III SYSTEMATIC DESCRIPTIONS

Class *SELACHII*

Order HYBODONTIFORMES

Family **HYBODONTIDAE** Owen 1846

DIAGNOSIS. See Berg (1955 : 61)

Genus ***HYBODUS*** Agassiz 1837 : 41

DIAGNOSIS. See Smith Woodward (1916: 3), but delete 'palatoquadrate not articulated with the postorbital region of the skull'.

TYPE SPECIES. *Hybodus reticulatus* Agassiz.

H. basanus Egerton, *H. ensis* Smith Woodward and *H. parvidens* Smith Woodward, the three species of the genus known by teeth in the British Wealden, are easily distinguished in the type material described by Smith Woodward but appear to be linked by intermediate forms in the new material. *H. basanus* is the only species of the three in which the complete dentition is known, and will be described first.

Hybodus basanus Egerton

(Pl. 1, fig. 1; Text-figs. 1–3)

1845 *Hybodus basanus* Egerton: 197, pl. 4.
1889 *Hybodus basanus* Egerton; Smith Woodward: 273, pl. 12, figs. 1–5.
1891 *Hybodus basanus* Egerton; Smith Woodward: 63, pl. 1, pl. 2, fig. 1.
1898 *Orthybodus basanus* (Egerton) Jaekel: 139.
1916 *Hybodus basanus* Egerton; Smith Woodward: 5, pl. 1, figs. 1, 2; pl. 2, fig. 1; text-figs. 3–5.
1919 *Hybodus basanus* Egerton; Smith Woodward: 139, pl. 26, fig. 3.

Amended diagnosis. *Hybodus* known by skull, dentition, fin spines and fragments of postcranial skeleton; nine or ten files of teeth in each ramus of the jaws, symphysial file present in lower jaw, dentition weakly heterodont; teeth reaching 15 mm. in length, central cusp high, slender (ratio of height above root/crown junction to length 1·0–2·0) and arched lingually; three or (rarely) four pairs of lateral cusps; labial face of crown with rather numerous fine striae, often bifurcated basally, reaching tips of lateral cusps and covering from one-third to two-thirds of central cusp; lingual face of crown with similar but longer striae almost reaching tip of central cusp; teeth without accessory cusps on the labial or lingual margins; root low, bent lingually; a single pair of cephalic spines with terminal barb; fin spines slender, compressed, not much arched, reaching about 20 cm. in length, lateral faces with 8–12 fine, sharp ridges, posterior denticles in two series, small and closely set.

Holotype. GSM No. 27973, Geological Survey & Museum, London, from the Weald Clay of Atherfield, Isle of Wight.

Material. In addition to the holotype, about twenty skulls, fragments of vertebral column, fin spines and isolated teeth in the British Museum (Natural History) and the Geological Survey & Museum.

Horizon and localities. Weald Clay: Atherfield, Isle of Wight; Pevensey Bay, Sussex; Henfield, Sussex; Bexhill, Sussex.

Description. *Hybodus basanus* is the only species of the genus in which the skull is well known. Smith Woodward (1916) has given a good description of the skull based on several well preserved heads in the British Museum (Natural History). Of the palato-quadrate he writes 'it can scarcely have articulated with the postorbital prominence of the neurocranium'. Smith (1942: 701) has questioned this, noting that in the Liassic *H. hauffianus* Fraas the skull is said to be amphistylic by Jaekel, and that it is amphistylic in *Synechodus*. Berg (1955: 62) has also suggested that Smith Woodward's observation needs checking. I have examined all of the skulls of *H. basanus* in the British Museum (Natural History). The palatoquadrate and hyomandibular are best shown in P.2082*a* and P.6103. There can be no doubt that Smith Woodward's reconstruction (1916, text-fig. 3) is accurate in showing the hyomandibular as being large and much higher than the postorbital part of the palatoquadrate. In this *H. basanus* differs from typical amphistylic sharks such as *Hexanchus*, where the hyomandibular is slender and no higher than the otic process

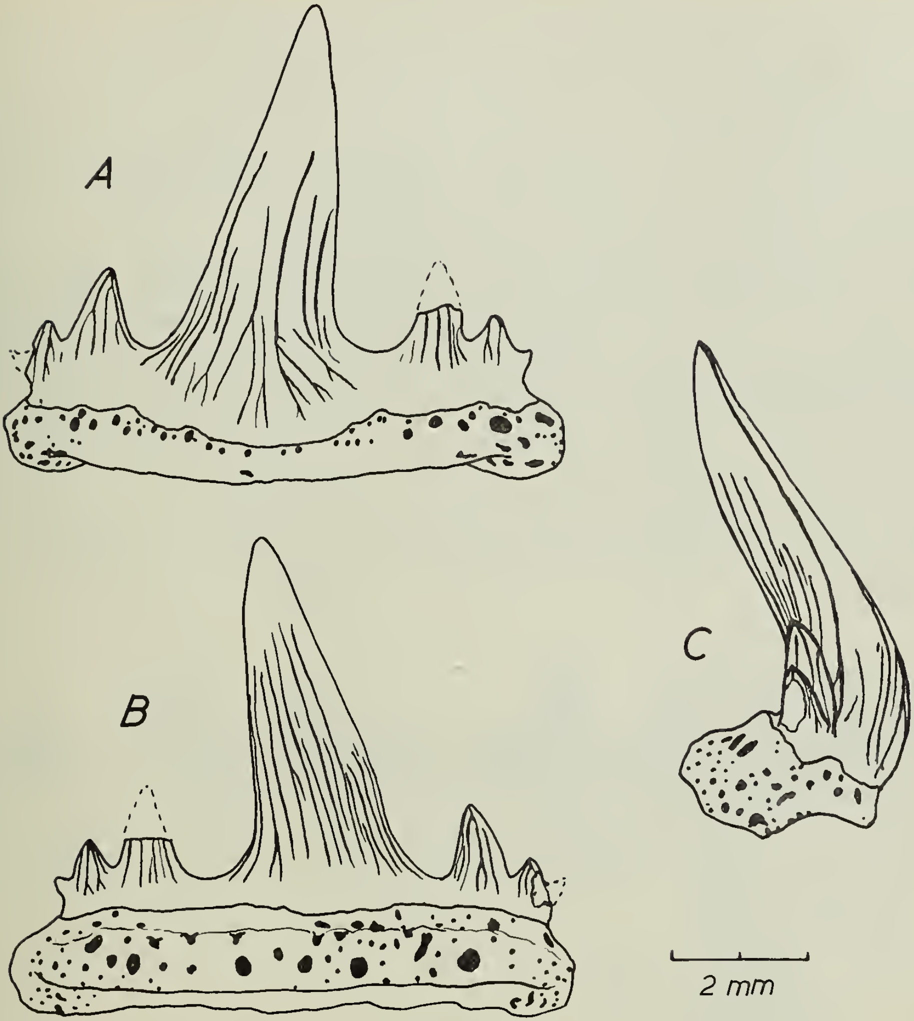


FIG. 1. *Hybodus basanus* Egerton. Tooth from the first or second file of the upper jaw, right side, in labial (A), lingual (B) and medial (C) view. P.11871, Weald Clay; Pevensey Bay, Sussex.

of the palatoquadrate, and from *Heterodontus* and *Hybodus hauffianus* (Jaekel 1906) in which the hyomandibular is stout but equal in height to the otic process of the palatoquadrate. I do not think it is possible, however, to decide whether the palatoquadrate of *H. basanus* had a post-orbital articulation or not. The otic process was certainly tucked well up below the postorbital process of the neurocranium, but there is no sign of an articular facet or condyle on the otic process.

It is possible that the suspension was amphistylic, but the long, large hyomandibular shows that the species tends towards the hyostylic condition.

Smith Woodward describes the dentition of *H. basanus* as consisting of ten or eleven paired files of teeth in each jaw, with a symphysial file in the mandible. The teeth (Text-fig. 1) have a high, slender central cusp and three pairs of lateral cusps which are well separated from the central cusp. The height of the central cusp (above the root/crown junction) is only slightly less than the length of the tooth in anterior teeth, but the height decreases posteriorly.

The central cusp curves lingually rather strongly, but the tip curves labially again, giving a weakly sigmoid outline to the cusp in medial view (Text-fig. 1B). Of the three pairs of lateral cusps, the innermost is sharply pointed, striated to its tip, and normally about one-third as high as the central cusp. The second pair of lateral cusps is shorter but similarly ornamented. The outermost cusps are normally very small and almost smooth. A minute fourth lateral cusp is occasionally present.

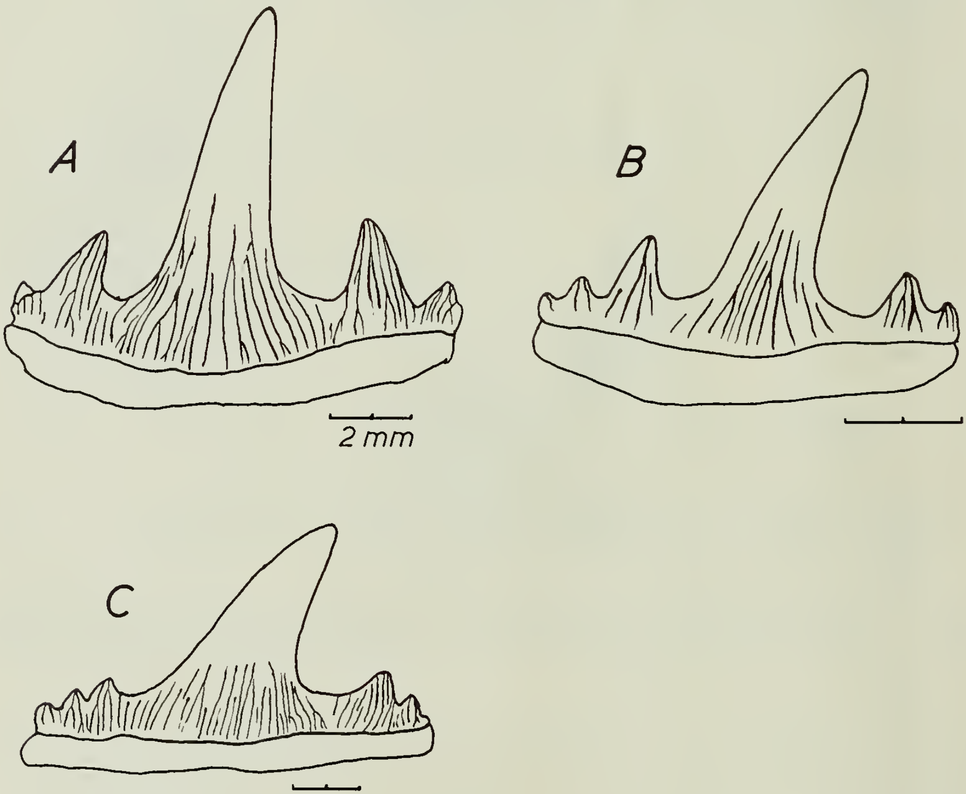


FIG. 2. *Hybodus basanus* Egerton. A. Tooth from the first file of the upper jaw, right side, in labial view. P.2082. B. Tooth from the sixth file of the lower jaw, left side, in labial view. P.6356. C. Tooth from the eighth file of the lower jaw, left side, in labial view. P.2082*b*. All from the Weald Clay of Pevensey Bay, Sussex.

The base of the labial face of the crown is ornamented with moderately fine, parallel or sub-parallel vertical striae, often bifurcating basally, which extend to the tips of the lateral cusps and to about one-third or half of the height of the central cusp. There is a good deal of variation in the strength, number and length of these striae: they are closely packed, weak and short in some fish (P.2082*b*, Text-fig. 2C), and coarse, well spaced and long, covering more than half the labial face of the central cusp, in others (P.11871, Text-fig. 1A). On the lingual face of the crown the ridges are stronger, and extend almost to the tip of the central cusp (P.2082*a*, P.11871, Text-fig. 1B). The root is low, and is turned lingually, with the labial face of the root lying almost at right angles to the axis of the central cusp. This description is based on the teeth of the complete skulls from the Weald Clay of Pevensey Bay, Sussex, and Atherfield, Isle of Wight.

It is difficult to match these teeth exactly in material from any other Wealden horizon or locality. In the new material from the Weald Clay of Henfield, which is approximately contemporary with the type material of *H. basanus*, there is a number of teeth of the type shown in Pl. 1, fig. 1 and Text-fig. 3. In these teeth the crown is lower than in those from the complete skulls of *H. basanus*, with a ratio of height (above the root/crown junction) to length of little less than 2·0, the striae are less numerous and are longer, reaching well over half the height of the central

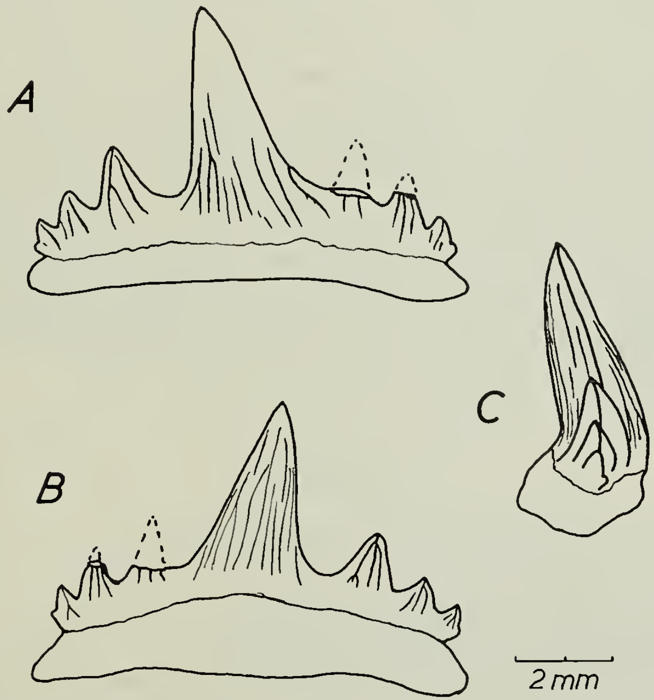


FIG. 3. *Hybodus basanus* Egerton. Lateral tooth in lingual (A), distal (B) and labial (C) view. P.46921, Weald Clay; Henfield, Sussex.

cusp on the labial face (the tooth shown in Text-fig. 3 has shorter striae than most teeth from Henfield) and to the tip of the cusp on the lingual face, and both the central cusp and the root are not turned lingually so strongly as they are in typical *H. basanus* (cf. Text-figs. 1C, 3C). In all these features the teeth from Henfield are intermediate between typical *H. basanus* from Atherfield and Pevensey, and typical teeth of *H. parvidens* from the Ashdown Beds and Wadhurst Clay (Text-figs. 6, 7). The Henfield teeth are referred to *H. basanus* rather than *H. parvidens* because they never show the knob or accessory cusp at the base of the labial face of the central cusp which is common in *H. parvidens*, because the striae are almost as numerous as they are in *H. basanus* and only rarely reach the tip of the central cusp, and because there is a difference in the extent of the striae on the labial and lingual faces of the central cusp (in *H. parvidens* the length of the striae is similar on the two faces of the central cusp).

No teeth referable to *H. basanus* are known from horizons above or below the Weald Clay. The tooth from the Lower Cretaceous of Japan referred to *H. basanus* by Yabe & Obata (1930 : 4, pl. 2, fig. 3) differs from this species in the longer and more slender central cusp and in the almost complete lack of striae on the labial face : it is possibly a *Synechodus*. Leriche (1911 : 457, pl. 6, fig. 2) has referred to *H. basanus* a fragment of fin spine from the Lower Neocomian of the Paris Basin, but this identification is very doubtful : the fragment could as well belong to another species.

Affinities. Smith Woodward (1916 : 10) considered that teeth and spines from horizons in the lower part of the Wealden showed resemblances to *H. basanus* without being referable to the species. These forms (see p. 294) are here included in *H. ensis* which in the Wealden seems to trend towards *H. basanus* in the form of the teeth, but is probably not related. Teeth of *H. basanus* from Henfield are intermediate in a number of characters between more typical teeth of the species from Pevensey and the Isle of Wight, and teeth of *H. parvidens* from lower horizons. This, together with the trend towards *H. basanus* shown by *H. parvidens* in the Grinstead Clay (see p. 299), leaves little doubt that *H. basanus* is a species confined to the Weald Clay (probably to the upper part alone) which evolved directly from *H. parvidens* by increase in size, in crown height and in the number of striae.

Hybodus ensis Smith Woodward

(Text-figs. 4, 5)

1889 *Hybodus* sp. inc. (? *strictus* Agassiz) Smith Woodward : 275.
1889 *Hybodus* sp. inc. (? *striatulus* Agassiz) Smith Woodward : 276, pl. 11, figs. 14, 15.
1916 *Hybodus ensis* Smith Woodward : 11, pl. 2, figs. 2–6 ; *non* fig. 7.

Amended diagnosis. *Hybodus* known only by isolated teeth : teeth large, up to 2 cm. in length, central cusp high (ratio of height above root/crown junction to length 1·0–1·5), broad at base, evenly tapering and moderately compressed, not much arched lingually ; two pairs of lateral cusps, inner lateral cusps moderately high, slender, pointed, well marked off from central cusp but close to it ; labial face of

crown with many fine, parallel striae reaching tips of lateral cusps but covering only basal quarter or fifth of central cusp; lingual face of crown with coarser striae extending about half way up central cusp; root low, bent lingually.

Holotype. BMNH No. 21349 (Smith Woodward, 1916, pl. 2, fig. 6), tooth without root, Middle Purbeck; Swanage, Dorset.

Material. In addition to the holotype, about one hundred isolated and fragmentary teeth.

Horizons and localities. Middle Purbeck: Swanage, Dorset. Upper Purbeck: Friar Waddon, Dorset. Ashdown Beds: Cliff End, Sussex. Wadhurst Clay: Teigh Farm, Stone, Kent; Hastings, Sussex. Grinstead Clay: Paddockhurst Park, Sussex; Tilgate Forest, Sussex.

Description. Smith Woodward based this species on incomplete teeth from the Middle Purbeck of Dorset, but also recorded it from the Wealden of Tilgate Forest (Grinstead Clay—see p. 294). All the specimens labelled as *H. ensis* by Smith Woodward are from the Purbeck.

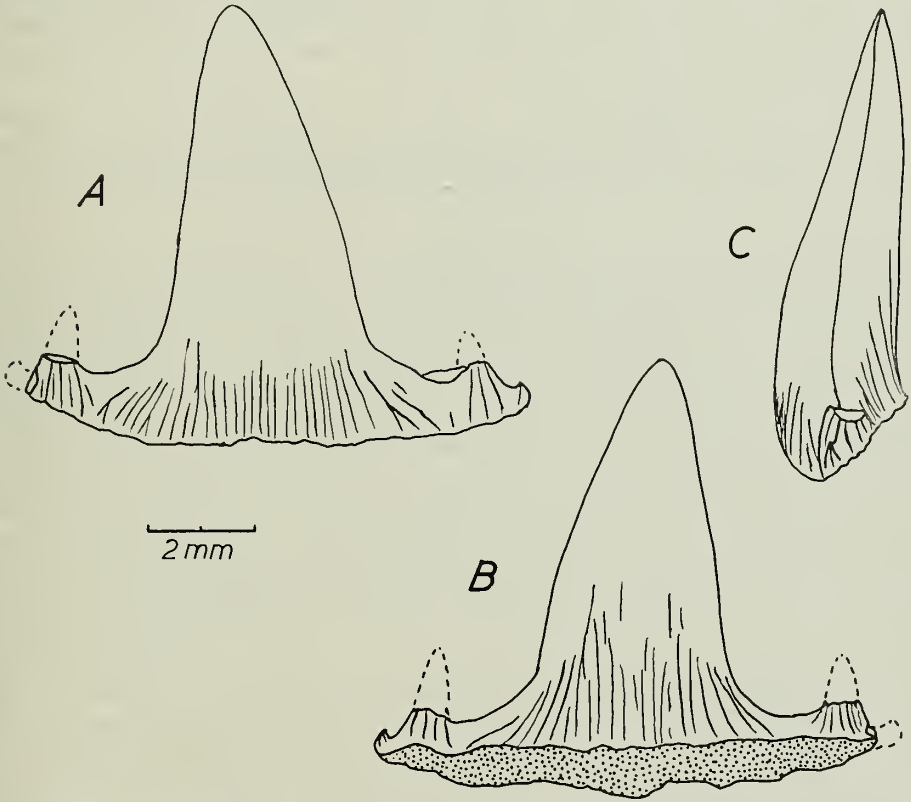


Fig. 4. *Hybodus ensis* Smith Woodward. Tooth in labial (A), lingual (B) and medial (C) view. 21349*c*, Middle Purbeck; Swanage, Dorset.

The species is poorly known, the Purbeckian type material consisting of teeth without roots exposed in labial view. One of these teeth, 21349*c*, has been removed from the matrix to expose the lingual face (Text-fig. 4). In the Purbeck material of *H. ensis* the crown is about as high as in *H. basanus*, with the ratio of length to height (above the root/crown junction) about 1·0, but the central cusp is much broader, the ratio of the breadth at its middle point to its height ranging from 2·8 to 3·0, compared with 4·0 to 5·0 in *H. basanus*. In no specimen of *H. ensis* are there more than two pairs of lateral cusps (21349*b*, Smith Woodward 1916, pl. 2, fig. 7, has three pairs of lateral cusps but does not belong in *H. ensis*—see *H. parvidens*, p. 297). In *H. ensis* the labial face of the crown (Text-fig. 4A) bears fine, close packed, parallel striae which extend almost to the tips of the inner lateral cusps but cover only the basal one-fifth or quarter of the central cusp. On the lingual face of the crown (Text-fig. 4B) the striae are less numerous, a little coarser and cover almost one-third of the height of the central cusp. The central cusp curves lingually less strongly than it does in *H. basanus* (cf. Text-figs. 1C, 4C). Other apparent differences between *H. ensis* and *H. basanus* suggested in Smith Woodward's original description—that the inner lateral cusps are higher and closer to the central cusp in *H. ensis*, and that the ratio of height to length of the tooth is greater in this species—are not confirmed by measurement of the teeth.

In 1889 (p. 276) Smith Woodward catalogued as '*Hybodus* sp. inc. (? *striatulus* Agassiz)' about thirty teeth from the Wealden of Tilgate Forest,[1] noting the high, moderately broad central cusp, the high, slender inner lateral cusps, and the striae 'rarely extending more than half the height of the median cone'. In 1916 (p. 10) he referred to these teeth as 'of the same general type as those of *H. basanus* . . . but not sufficiently similar to be referred with certainty to this species'. Most of these teeth are more or less rolled and waterworn, and many are quite indeterminable. Some, such as 48377 (Tilgate Forest) and P.6353 (Hastings, unknown horizon) agree exactly with the Purbeck specimens of *H. ensis*, and leave no doubt that this species extended into the Wealden. But the majority of these teeth do not agree exactly with the type material of *H. ensis* : 2693 (Tilgate Forest, Text-fig. 5, Smith Woodward 1889, pl. 11, fig. 14) is the best preserved of these, and is typical in shape. These teeth differ from *H. ensis* in the more slender, sharply pointed central cusp (ratio of breadth measured at the middle point to height *c.* 3·5), but they agree with *H. ensis* and differ from *H. basanus* in their large size, weakly arched central cusp (Text-fig. 5B), two pairs of lateral cusps, in the short, fine striae on the labial face of the crown, rarely reaching more than one-third of the height of the central cusp, and in the short striae on the lingual face of the crown. The striae on the lingual face of the central cusp extend about as far as they do in typical *H. ensis*, and are characteristically longer near the margins of the cusp than they are in the centre. In my opinion these teeth should be included in *H. ensis*. Some of these Wealden teeth (26026 ; Smith Woodward 1889, pl. 11, fig. 14 : 26024, both from Tilgate Forest)

[1] Mantell's horizon at Tilgate Forest, previously thought to lie in the Upper Tunbridge Wells Sand, directly below the Weald Clay (Topley 1875 : 92), has recently been re-identified as in the Cuckfield Stone, in the middle part of the Grinstead Clay (Stubblefield 1963 : 37).

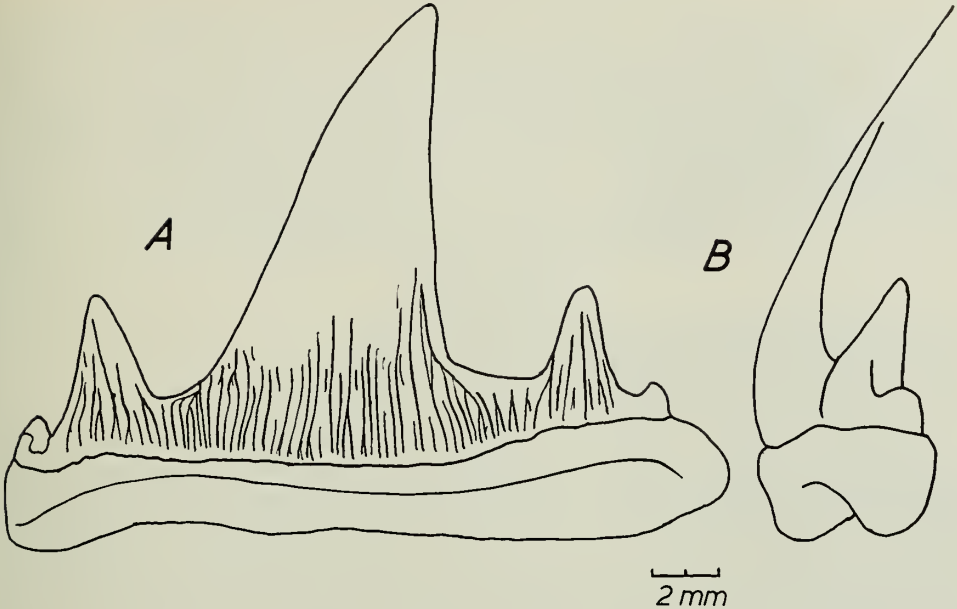


FIG. 5. *Hybodus ensis* Smith Woodward. Tooth in labial (A) and medial (B) view. 2693, Grinstead Clay ; Tilgate Forest, Sussex.

tend towards *H. basanus* in having a more slender central cusp with rather coarse striae covering almost half of the labial face, but they have only two pairs of lateral cusps : 26024 is particularly like the typical Weald Clay *H. basanus*, but it seems probable that it is not an early example of this species but a tooth of *H. ensis* in which the evident trend towards narrowing of the central cusp and extension and coarsening of the ornament has gone farther than in other examples.

Among the new material from the Cliff End and Paddockhurst bone-beds there are no complete large teeth, but isolated central cusps and imperfect crowns are very common. All of these large teeth can be referred to *H. ensis* : they show a range in breadth of the central cusp from stout forms like the Purbeck *H. ensis* to slender forms approaching the proportions of *H. basanus*, but the striae on the labial face are always short, fine and closely packed, and on the lingual face they are always shorter than in *H. basanus* and are longer at the margins of the central cusp than in the centre.

No examples of *H. ensis* are known from horizons above the Grinstead Clay.

AFFINITIES. *H. ensis* is a species which ranges from the Middle Purbeck to the Grinstead Clay (Paddockhurst bone-bed and Tilgate Forest). In the Wealden the teeth show a trend towards narrowing of the central cusp, sometimes accompanied by coarsening and lengthening of the striae which may produce teeth closely similar to those of *H. basanus* in shape.

Smith Woodward (1916 : 11) noted the similarity between the Purbeck forms of *H. ensis* and the Middle and Upper Jurassic *H. grossiconus* Agassiz. Extremely similar to *H. ensis* is *H. songaensis* Saint-Seine (1962 : 4, pl. 6, fig. 6), a species based on a single tooth from the Songa Beds of the Congo, probably marine and of Kimmeridgian age, which could well be synonymous with *H. ensis*. *H. ensis* is possibly derived directly from these marine Jurassic forms.

Hybodus parvidens Smith Woodward

(Text-figs. 6–9)

1889 *Hybodus* sp. inc. Smith Woodward : 276, pl. 11, fig. 16.
1916 *Hybodus ensis* Smith Woodward : pl. 2, fig. 7 (*errore*).
1916 *Hybodus parvidens* Smith Woodward : 12, pl. 2, figs. 8–14.
1949 *Hybodus parvidens* Smith Woodward ; Allen : 277 (name only).

Amended diagnosis. *Hybodus* known only by isolated teeth : teeth small, less than 10 mm. in length ; central cusp moderately high, not much compressed, lower and broader in posterior teeth ; ratio of height of central cusp (above root/crown junction) to length of tooth between 1·5 and 3·0 ; three or four pairs of lateral cusps ; labial face of crown with few coarse striae, often bifurcating basally, which reach the tips of the lateral cusps and commonly reach the tip of the central cusp except in some high anterior teeth, striae on lingual face similar ; knob or accessory cusp frequently present at base of labial surface of central cusp, no other accessory cusps ; root moderately deep, turned lingually a little.

Holotype. BMNH P.11877, tooth without root, Wadhurst Clay, Hastings.

Material. About two hundred isolated teeth.

Horizons and localities. Middle Purbeck : Swanage, Dorset. Upper Purbeck : Friar Waddon, Dorset. Ashdown Beds : Cliff End, Sussex ; Fairlight, Sussex. Wadhurst Clay : Teigh Farm, Stone, Kent ; Hastings, Sussex ; Rye, Sussex. Grinstead Clay : Paddockhurst Park, Sussex ; Tilgate Forest, Sussex. Weald Clay : Henfield, Sussex.

Description. Smith Woodward based this species on incomplete teeth from the Wadhurst Clay, in none of which was the root preserved. The holotype and two of the paratypes are shown in Text-fig. 6. Among the new material from the Cliff End bone-bed there are several more or less complete and unworn teeth (Text-fig. 7). The high-crowned teeth (Text-figs. 6, 7A) are presumably anterior, the low-crowned (Text-fig. 7B) posterior.

In this typical material from the Ashdown Beds and Wadhurst Clay, the central cusp is moderately high in anterior teeth, with a ratio of height of cusp to length of tooth of about 1·8–2·0. In posterior teeth the central cusp becomes much lower, the ratio of height to length reaching about 3·0. The central cusp is not compressed as it is in *H. ensis* and *H. basanus*, and does not curve lingually. There are always three pairs of lateral cusps, and often four. On the labial face of the crown the striae are coarse, sparse, and often bifurcated basally. They reach the tips of the lateral cusps

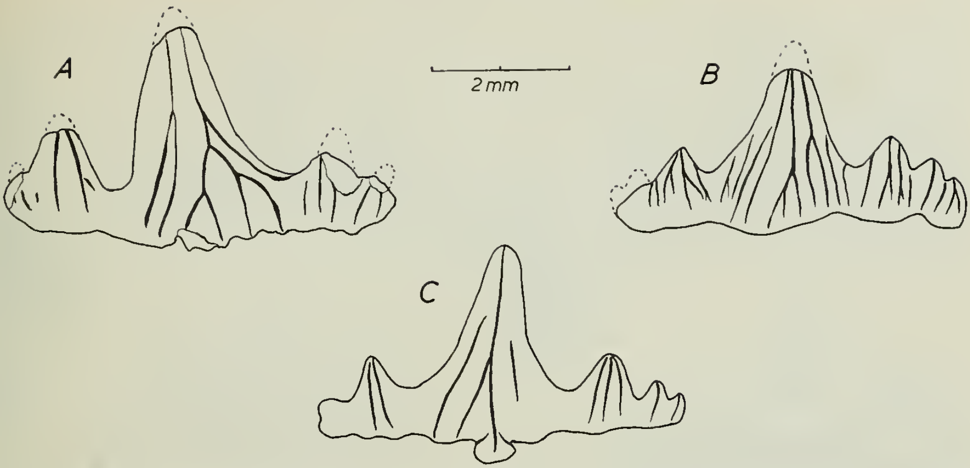


FIG. 6. *Hybodus parvidens* Smith Woodward. Teeth from the Wadhurst Clay of Hastings, Sussex, in labial view. A. P.11877, the holotype. B. P.11878 (paratype). C. P.11880 (paratype).

and commonly reach the tip of the central cusp : in a sample of 37 teeth from Cliff End, the central cusp is striated to its tip in 22 ; it is striated to the tip in 10 of 13 posterior teeth and in 12 of 24 anterior teeth. On the lingual face of the crown the ornament is very similar. It is interesting to note that in low-crowned posterior teeth, the striae on the lingual face of the crown tend to anastomose basally and form a reticular pattern (Text-fig. 7B) approaching the pattern found in this region in low-crowned species like *H. delabechei* and *H. brevicostatus* (Text-fig. 10). At the base of the labial face of the central cusp a knob or accessory cusp is very commonly present. This accessory cusp is larger and more sharply defined in posterior teeth than in anterior (cf. Text-fig. 7A, B). In the Cliff End material this accessory cusp is present in more than half the teeth (in 28 of a sample of 40), and is commoner in posterior teeth (present in 13 of 16 posterior teeth and in 15 of 24 anterior teeth). The root in *H. parvidens* is typically hybodont, with foramina irregularly distributed on both surfaces, is moderately deep, and is turned lingually a little (Text-fig. 7).

The above description is based on teeth from the Lower Wealden Ashdown Beds and Wadhurst Clay. Smith Woodward (1916 : 12) also recorded the species from the Weald Clay of Berwick, Sussex, but I have been unable to trace the specimen on which this record was based : it was probably an example of *H. brevicostatus*. *H. parvidens* also occurs in the Purbeck, as is shown by a sample of sixteen incomplete teeth from Friar Waddon, Dorset, and by 21349*b* and 21349*d*, two teeth from the Middle Purbeck of Swanage, the first figured as *H. ensis* by Smith Woodward (1916, pl. 2, fig. 7). The picture presented by these Purbeck teeth (Text-fig. 8) is rather different from that in the Wealden material described above. The Purbeck teeth agree with the Wealden forms in size, but in most of them the crown is rather high, and where the ratio of crown height to tooth length is measurable (21349*b*, *d*) it is

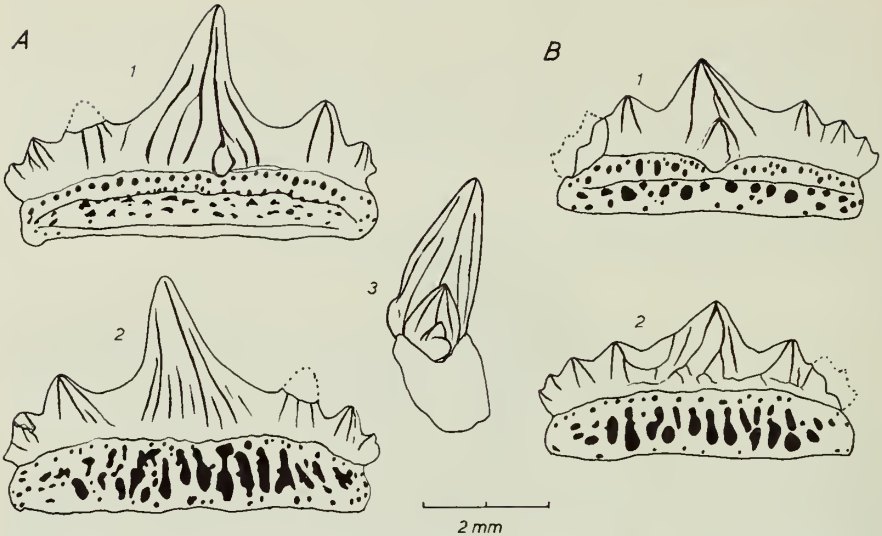


FIG. 7. *Hybodus parvidens* Smith Woodward. An anterior (A) and a posterior (B) tooth in labial (1), lingual (2) and medial (3) view. P.46930–31, Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex.

lower (1·5–1·7) than is usual in Wealden teeth. The striae on the labial face of the central cusp reach the tip in only four of the eighteen teeth: in six they cover between two-thirds and three-quarters of the cusp, in four about half the cusp, and in four less than half. Also, there is no accessory cusp at the base of the central cusp in any of the teeth, though there is an incipient cusp in two of them (Text-fig. 8B). But in spite of these differences, I have little doubt in referring these teeth to *H. parvidens*: the examples with lower crowns exactly match those typical *H. parvidens* in which the accessory cusp is absent.

FIG. 8. *Hybodus parvidens* Smith Woodward. Fragmentary teeth in labial view. A. 21349*d*, Purbeck; Swanage, Dorset. B. P.46959, Upper Purbeck; Friar Waddon, Dorset.

Among the material from the Paddockhurst bone-bed (Grinstead Clay) complete teeth are rare, but small central cusps and incomplete teeth (Text-fig. 9A) are common. Teeth of *H. parvidens* which agree with the typical forms from the Ashdown Beds and Wadhurst Clay occur, but are rather rare. In a sample of 37 teeth, four are typical low-crowned posterior teeth of *H. parvidens*, the other 33 are high-crowned forms. Of these 33 teeth, only three are striated to the tip of the central cusp (cf. 12 out of 24 in high-crowned teeth from Cliff End), and only three have an accessory cusp (cf. 15 out of 24 at Cliff End). The striae in these teeth also tend to be finer and more numerous than in typical *H. parvidens*.

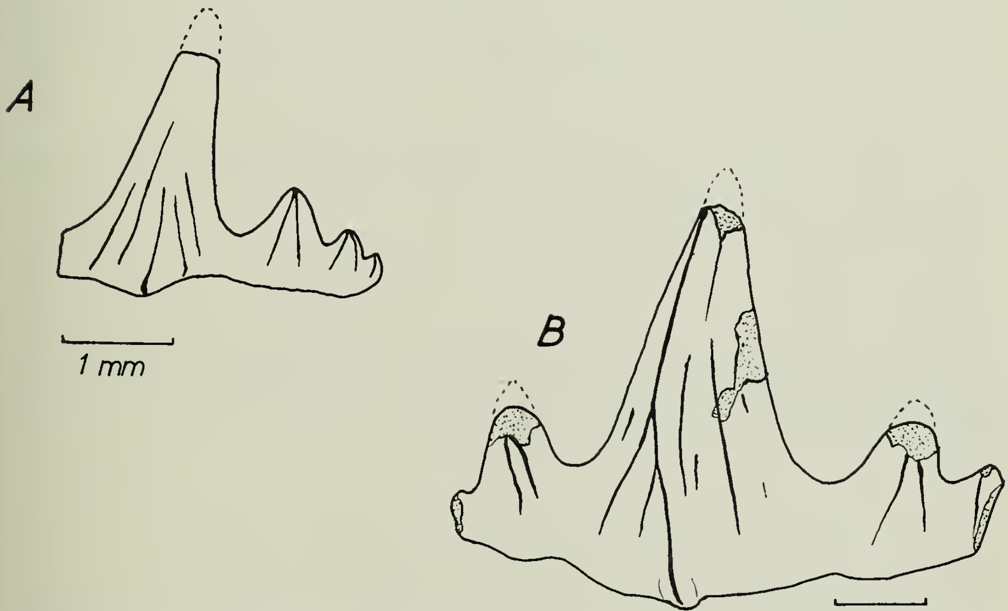


Fig. 9. *Hybodus parvidens* Smith Woodward. Teeth in labial view. A. P.46944, Grinstead Clay, Paddockhurst Bone-bed; Paddockhurst Park, Sussex. B. P.46971, Weald Clay; Henfield, Sussex.

Among the material from Tilgate Forest (Grinstead Clay) small teeth are very rare, but there are two examples of *H. parvidens*, 2850 and 3146.

Among the material from the Weald Clay of Henfield I can find only two teeth which are referable to *H. parvidens* (Text-fig. 9B); these are typical examples, very like teeth from the Grinstead Clay. Apart from these two specimens, all the high-crowned teeth from Henfield are of the type shown in Text-fig. 3, which are assigned to *H. basanus* for the reasons given on p. 292. The smaller low-crowned teeth (Text-fig. 13) are placed in *H. brevicostatus* for the reasons given on p. 306. *H. parvidens* is not known from any other locality in the Weald Clay or from any higher horizon.

Affinities. The various samples of teeth of *H. parvidens* described above suggest that the history of the species was as follows. The species first appeared in the

Middle Purbeck. Purbeckian teeth are rather high-crowned, with no accessory cusp and with rather short, fine striae. In the Lower Wealden (Ashdown Beds and Wadhurst Clay) the species reached its typical and most distinctive form, with a crown which is of moderate height and has both striae to its tip and an accessory cusp in the majority of teeth. In the Grinstead Clay the species seems to trend towards the Purbeck form again, with an increase in crown height, a reduction in the height and an increase in the number of the striae on the central cusp, and a reduction in the incidence of the accessory cusp. Only two undoubted examples of *H. parvidens* are known above the Grinstead Clay. It seems very probable that the species did not become extinct, but evolved into *H. basanus* by a further increase in crown height and in the number of striae, coupled with an increase in size. The increase in size which marks the transition to *H. basanus* in the Weald Clay is perhaps correlated with the apparent extinction of the large-toothed *H. ensis* shortly before the Weald Clay was deposited.

It is shown below (p. 308) that the Wealden (Ashdown Beds to Weald Clay) species *H. brevicostatus* is also probably an offshoot of *H. parvidens* which originated near the base of the Wealden.

Smith Woodward (1916 : 12) suggested a possible relationship between *H. parvidens* and the Upper Jurassic *H. obtusus*, a species in which the crown is moderately high, coarsely striated, and in which accessory cusps are very common. But the form of the earliest examples of *H. parvidens* in the Purbeck, where there is no accessory cusp and where the crown is higher and less strongly striated than it is in the typical forms, suggests that the species did not originate from *H. obtusus* but from some unknown small, high-crowned species in the Upper Jurassic.

Hybodus brevicostatus sp. nov.

(Pl. 1, fig. 3 ; Pl. 2 ; Pl. 3, figs. 1–3 : Text-figs. 10–13)

DIAGNOSIS. *Hybodus* known by almost complete dentition and fin spines : nine paired files and a median symphysial file probably present in each jaw, dentition moderately heterodont ; teeth ranging (in one individual) from 8·0–18·5 mm. in length ; crown low and long, ratio of crown height (above the root/crown junction) to tooth length 3·25–6·25, crown not deeper than the root ; central cusp low, lateral cusps four or more, sometimes not recognizable in posterior and lateral teeth ; several accessory cusps often present on both labial and lingual margins of the crown, especially in the lower jaw ; crown with longitudinal occlusal crest and many coarse striae, often bifurcating basally, which reach the tips of the cusps and are interspersed in larger teeth with finer striae which fail to reach the tips of the cusps ; at the base of the lingual face of the crown the striae anastomose in a reticular pattern ; root deep, not turned lingually. Fin spines reaching about 18 cm. in length ; anterior edge keeled, lateral faces with 8–10 narrow, well spaced, discontinuous striae, posterior face with raised band bearing recurved denticles which lie in a single irregular series with occasional doubling, denticles extending proximally beyond the limit of the striae on the lateral surfaces.

HOLOTYPE. BMNH no. P.46973 (Pl. 2 ; Pl. 3, figs. 1, 3), sixty-six teeth, fragments of calcified cartilage and an incomplete dorsal fin spine, the remains of a single individual, from the Weald Clay of Henfield, Sussex.

MATERIAL. In addition to the holotype, thirty isolated teeth and a fin spine.

HORIZONS AND LOCALITIES. Ashdown Beds : Cliff End bone-bed, Sussex. Wadhurst Clay : Hastings, Sussex. Grinstead Clay : Paddockhurst bone-bed, Sussex; Tilgate Forest, Sussex. Weald Clay : Henfield, Sussex ; Bookhurst, Surrey. Wealden Shales ; Atherfield Point and Cowleaze Chine, Isle of Wight.

DESCRIPTION. The holotype was found in 1962 by Mr. J. F. Wyley immediately above the '*Paludina*' limestone in the north-east corner of the Henfield pit. The teeth, calcified cartilage and fin spine were collected from an area of about two square feet : the bulk of the material was collected at one time but a few teeth have been found at the same point by Mr. Wyley in subsequent visits to the pit. There can be no doubt that this material represents the remains of a single individual. Since this is the first specimen of *Hybodus* in which it is possible accurately to reconstruct the dentition with teeth free from matrix, and in which the upper and lower teeth can be distinguished, it will be described in some detail.

1. *The Dentition*

The teeth of the holotype were not found in natural association, but it has proved possible to reconstruct at least the anterior parts of the dentition with some accuracy. The teeth can be sorted into 'left' and 'right' (treating all the teeth as if they are from one jaw) by the asymmetry of the cusps, which point away from the symphysis in *Hybodus*, and by the asymmetry of the root. Many of the teeth can be matched with others to reconstruct successional files, and these files can be placed approximately in their position in the mouth by the degree of asymmetry of the crown, and by the relative height and length of the teeth. When this had been done, of the fifty-seven more complete teeth four were median, twenty-three 'left' and thirty 'right', and there appeared to be fourteen successional files, containing from two to eight teeth. Fourteen teeth could not be matched with any others. In these fourteen 'series', the measurements length of crown, length of root, depth of tooth, depth of crown, depth of root, breadth of crown and breadth of root were taken on each tooth (Table I), and the range of each measurement in each series was plotted against the inferred position in the mouth. The fourteen unmatched teeth were then measured and allocated their position in the mouth by reference to the plot. When this had been done it was clear that in each of the better represented tooth series there were two types of teeth : these represent the upper and lower jaws (see p. 303).

General Features of the Dentition

The dentition of *H. brevicostatus* (Text-fig. 10, Pl. 2) consists of a symphysial file of teeth in each jaw and probably nine paired files in each jaw. The largest teeth are the fifth paired file. In general features, the teeth are very like those of the Lower

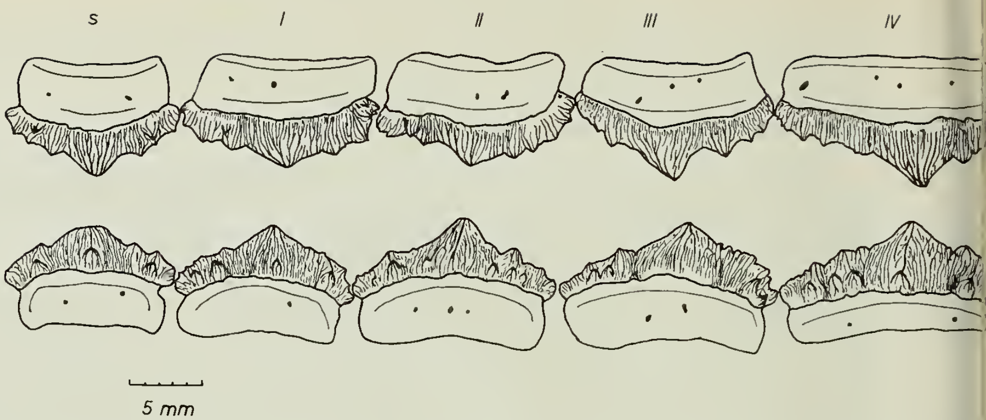


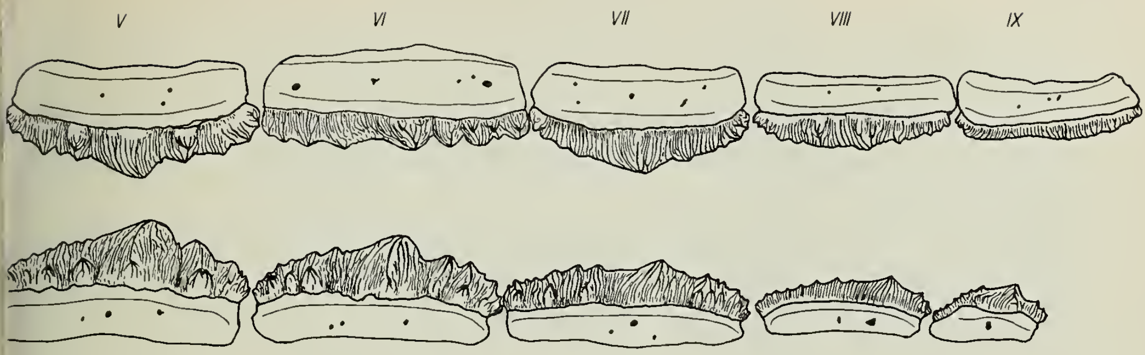
FIG. 10. *Hybodus brevicostatus* sp. nov. Restoration of the dentition of the left side in labi
VII and VIII in the upper jaw and III, VII and IX in the lower jaw are reversed drawing

Liassic *H. delabechei* Charlesworth (Smith Woodward 1889, pl. 10, figs. 1–5), with which they share a low crown, hardly exceeding the root in depth, a central cusp and four or more less conspicuous pairs of lateral cusps, and the ornament of very numerous prominent striae. The central cusp lies at or near the centre of the tooth in all but the most posterior files (Text-fig. 10, VIII and IX; Pl. 2, figs. 5, 6), where it may be strongly eccentric or unrecognizable. The number of lateral cusps is normally four on each side, but in the lateral and posterior teeth the lateral cusps may be more numerous or not recognizable. Accessory cusps occur very commonly on both the lingual and labial margins of the crown, particularly on the labial face of the mandibular teeth (see p. 305).

There is a sharp occlusal crest running the length of the tooth from which strong striae pass to the base of the crown. These main striae often bifurcate basally, and between them there are weaker striae which fail to reach the occlusal crest. There is no significant difference between the strength of the striae on the labial and lingual faces of the crown : in some teeth they are stronger on the lingual face, in others on the labial. At the base of the lingual face of the crown the ridges anastomose in a reticular pattern. There is a good deal of variation in the ornament of the crown from one tooth to another, but this variation seems to have no significance between one jaw and the other or between tooth files.

The roots of the teeth are typically hybodontoid (Casier 1947*a* : 9). In all the teeth the root is moderately compressed, approximately equal to the crown both in depth and breadth, with a concave labial face and a flat or weakly convex lingual face. In all the teeth the root is without specialized foramina but has a large number of irregular foramina on both the lingual and labial faces.

In histological structure (Pl. 3, fig. 3) the teeth are again typical of *Hybodus* (Jaekel 1889, pl. 7, figs. 1, 4). The crown is covered by a well marked and rather thick layer of enamel which contains fine fibrils in its basal part. Below the enamel there is a



view. ' s ', symphysial file, I–IX, paired files. All teeth drawn from the holotype ; V, VI,
of teeth from the right side. P.46973, Weald Clay ; Henfield, Sussex.

layer of very regular pallial dentine which makes up about one-fifth of the thickness of the crown. Below the pallial dentine the tooth consists of normal osteodentine. In the crown the osteodentine is dense, with many slender vascular canals : in the root it is much more spongy, with large, anastomosing vascular canals.

Distinction between Upper and Lower Teeth

As noted above, when the teeth of the holotype had been assigned to their positions in the jaws, among the better represented series (the symphysial and first five paired series) teeth of two types could be recognized. These clearly represent the upper and lower jaws. The upper and lower teeth can normally be distinguished by features of both the root and the crown, but the most reliable characters are in the root. In one type of tooth (Text-fig. 11A) the labial face of the root is strongly concave, the base of the root is rounded, and there is normally a well marked furrow between root and crown on both labial and lingual faces of the tooth. In the second type of tooth (Text-fig. 11B) the labial face of the root is less strongly concave, the base of the root is flattened in a well marked oblique shelf, and there is normally a very weak furrow at the junction of root and crown. The flattening of the base of the root is

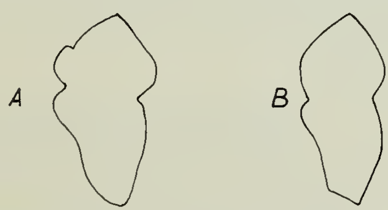


FIG. 11. *Hybodus brevicostatus* sp. nov. Diagrammatic transverse sections of teeth from the lower (A) and upper (B) jaws. $\times 3$.

TABLE I

The dimensions (in mm.) of the teeth of P.46973, the holotype of *Hybodus brevicostatus* sp. nov. Weald Clay, Henfield, Sussex

File		Number of teeth preserved	Length of crown-Range	Length of crown-Mean	Length of root-Mean	Total depth-Range	Total depth-Mean	Depth of crown-Mean	Depth of root-Mean	Breadth of crown-Range	Breadth of crown-Mean	Breadth of root-Mean	Length of crown / Total depth	Length of crown / Breadth of crown
Symphysial	upper	2	12·0–12·1	12·05	10·8	6·9–7·7	7·3	3·55	3·8	3·5–4·0	3·75	4·2	1·6	3·2
	lower	2	11·7–12·0	11·85	10·15	7·3–7·5	7·4	3·75	3·55	4·0–4·7	4·35	3·85	1·6	2·7
First	upper	4	12·1–13·8	13·05	11·8	7·9–8·0	7·95	3·85	4·0	3·5–3·9	3·7	4·15	1·6	3·5
	lower	7	12·1–13·5	12·8	11·7	7·6–8·2	7·9	3·8	3·95	3·8–4·3	4·05	4·05	1·6	3·1
Second	upper	6	13·8–14·3	14·1	12·6	7·5–8·3	7·9	4·0	4·05	3·2–4·0	3·7	4·05	1·8	3·8
	lower	4	13·9–14·8	14·2	13·05	8·0–8·3	8·15	4·2	3·95	4·1–4·5	4·25	4·05	1·7	3·3
Third	upper	2	13·8–14·7	14·25	13·75	8·2–8·5	8·35	4·4	4·0	3·6	3·6	4·05	1·7	4·0
	lower	5	14·8–15·2	15·05	13·85	7·8–8·5	8·2	4·25	4·1	4·0–4·6	4·2	4·5	1·8	3·6
Fourth	upper	3	15·7–16·8	16·25	15·35	8·0–9·0	8·5	4·4	4·2	3·6–3·9	3·8	3·9	1·9	4·3
	lower	4	15·7–16·4	16·0	14·7	7·6–8·7	8·0	4·5	4·0	4·1–4·6	4·35	4·0	2·0	3·7
Fifth	upper	5	17·7–18·3	18·0	16·7	7·6–8·0	7·8	4·05	3·9	3·1–4·3	3·9	4·0	2·3	4·6
	lower	1	18·6	18·6	17·3	8·6	8·6	4·6	4·1	4·8	4·8	4·6	2·2	3·9
Sixth	upper	2	19·0	19·0	18·3	7·6–7·8	7·7	3·9	3·8	3·8–3·9	3·85	4·0	2·5	4·9
	lower	2	17·8–18·1	17·95	17·15	8·0	8·0	3·95	4·2	4·0–4·3	4·15	3·95	2·3	4·3
Seventh	upper	2	15·2	15·2	14·95	6·0–7·1	6·55	3·2	3·45	3·1–3·5	3·3	3·45	2·3	4·6
	lower	1	16·9	16·9	16·3	6·0	6·0	3·0	3·1	3·2	3·2	3·1	2·8	5·3
Eighth	upper	3	13·7–13·9	13·8	13·35	4·5–5·9	5·1	2·5	2·7	2·1–2·9	2·4	2·4	2·7	5·7
	lower	1	12·0	12·0	11·0	4·0	4·0	2·0	2·0	1·9	1·9	2·2	3·0	6·3
Ninth	upper	1	12·5	12·5	12·2	4·2	4·2	2·0	2·1	2·0	2·0	2·8	3·0	6·2
	lower	1	7·8	7·8	7·2	3·8	3·8	1·9	2·1	2·3	2·3	2·6	2·0	3·4

the most reliable method of distinguishing between the two types of teeth (Pl. 2, cf. figs. 1*a*, 2*a*, and 3*a*, 4*a*). In the crown, those teeth with a rounded base to the root have significantly more accessory cusps on the margin of both labial and lingual faces. Taking only the teeth of the symphysial and first six paired files, accessory cusps are present on the labial face of all the teeth with a rounded base to the root. The number of accessory cusps on this face ranges from one to six, the mean being 4·1. On the lingual face of these teeth accessory cusps are present in seventeen teeth out of twenty-six (65%), with a range of 1–3 and a mean of 1·1. In teeth with a flattened base to the root, accessory cusps are present on the labial face in sixteen out of nineteen teeth (84%), with a range of 1–6 cusps and a mean of 1·7. On the lingual face of these teeth accessory cusps are present in six out of nineteen teeth (32%), with a range of 1–2 and a mean of 0·6. The presence of an accessory cusp at the base of the labial face of the central cusp is particularly characteristic of teeth with a rounded base to the root, and there is very rarely an accessory cusp in this position in teeth with a flattened base to the root. This is reflected in the maximum breadth of the crown (Table I) which is the only dimension in which there is a significant difference between the two types of teeth.

There is no absolutely reliable criterion by which these two types of teeth can be assigned to the upper or lower jaw, but comparison with associated dentitions of *Hybodus obtusus* from the Oxford Clay and with various species of *Hybodus* and *Acrodus* from the Lower Lias suggests that the teeth with the more numerous accessory cusps and the rounded base to the root are mandibular. The roots are visible in very few of the teeth in these associated dentitions, but comparison with isolated Jurassic teeth shows that the characters discussed above will serve to assign most teeth of *Acrodus* and low-crowned species of *Hybodus* to the appropriate jaw.

Variation in Teeth with Position in the Jaws

The main variations in the teeth from different parts of the jaws are clear from Text-fig. 10, Pl. 2 and Table I. The length and depth of both root and crown increase to a maximum in the middle of each jaw ramus, the length reaching a maximum at the fifth paired file in the lower jaw and the sixth in the upper, the depth at the fourth file in the upper jaw and the fifth in the mandible. The depth of the root exceeds that of the crown in the symphysial, first, seventh, eighth and ninth files. The maximum breadth of the crown exceeds that of the root in all but the last two files in the mandible, while in the upper jaw the breadth of the root is always greater than that of the crown.

Other Material

Teeth of *H. brevicostatus* first appear in the Ashdown Beds, and range through to the Wealden Shales, at the extreme top of the Wealden, but the species is rare throughout this time.

Among the material from the Cliff End bone-bed (Ashdown Beds) there are six more or less complete teeth of the species, the best preserved of which is shown in

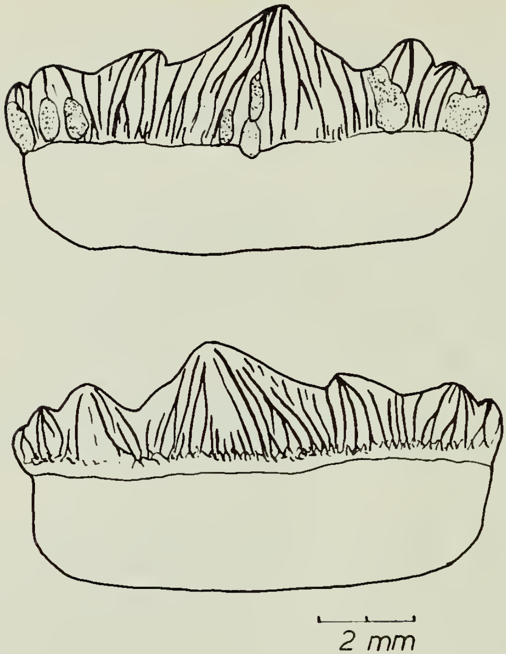


FIG. 12. *Hybodus brevicostatus* sp. nov. Tooth in labial (above) and lingual view. P.11891, Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex.

Text-fig. 12. All these teeth are smaller than those of the holotype, with a maximum length of about 10 mm., and they have fewer striae and fewer accessory cusps.

In the Wadhurst Clay *H. brevicostatus* is represented by a fragment of a small tooth (P.11875) and by P.11876 (Pl. 1, fig. 3), a large tooth, 15 mm. in length, probably a parasymphysial from the upper jaw, in which the crown is unusually high.

In the Grinstead Clay there are thirteen teeth of *H. brevicostatus* among the material from the Paddockhurst bone-bed. These are all small (less than 9 mm. in length), low-crowned forms. 26027 from Tilgate Forest is a larger (11 mm.) example, again a low-crowned posterior tooth.

Among the material from the Weald Clay of Henfield there is a number of teeth of *H. brevicostatus* in addition to the holotype. Most of these are normal teeth, as large as or a little smaller than those of the holotype, but two are very small examples (Text-fig. 13), P.46984, less than 6 mm. in length and P.46989, 4 mm. long. These small teeth agree with those of the holotype in shape and in the numerous accessory cusps, but in the few, coarse striae on the crown and in the clearly marked lateral cusps they resemble *H. parvidens*. One anterior tooth of *H. brevicostatus* (P.12812) is also known from the Weald Clay of Bookhurst, Surrey.

The latest occurrence of *H. brevicostatus* teeth is P.13341, an incomplete parasymphysial tooth from the Wealden Shales of Atherfield Point, Isle of Wight.

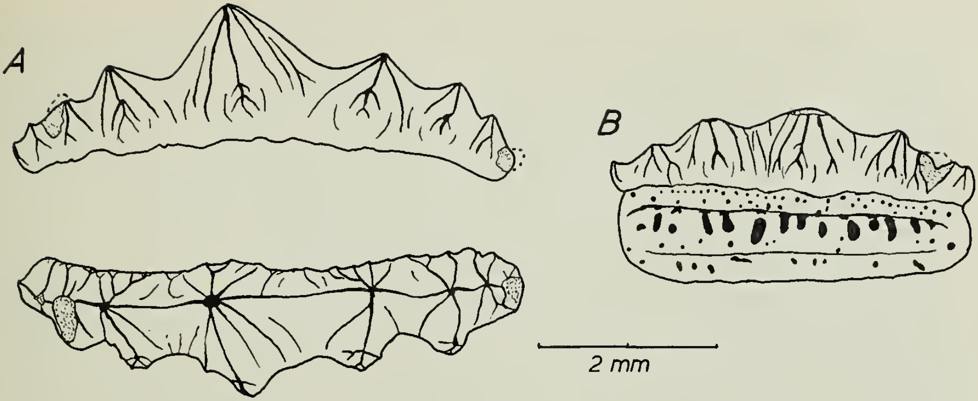


FIG. 13. *Hybodus brevicostatus* sp. nov. ? Juvenile teeth from the Weald Clay of Henfield, Sussex. A. P.46984 in labial (above) and occlusal view. B. P.46989 in labial view.

2. *Calcified Cartilage*

Together with the teeth of the holotype Mr. Wyley collected a number of fragments of heavily calcified cartilage. These include recognizable parts of the jaws and branchial arches, but they show nothing worthy of description.

3. *Fin Spines*

Found with the teeth and calcified cartilage of the holotype was a single incomplete fin spine (Pl. 3, fig. 1). The British Museum (Natural History) contains one spine which agrees with this, P.13268 from the Wealden Shales overlying the *Hypsilophodon* Bed, Cowleaze Chine, Isle of Wight (Pl. 3, fig. 2). These two spines agree almost exactly in size ; each must have had a total length of about 20 cm. Although they agree well in most characters, the angle of insertion of the Isle of Wight spine (inferred from the extent of the enamel ridges on the surface and the obliquity of the growth lines) was probably less than that of the Henfield spine. This suggests that the Isle of Wight specimen is an anterior fin spine and the Henfield is posterior, since in those hybodonts known by complete specimens the anterior fin spine lies more obliquely than the posterior (Brough 1935).

The most striking feature of these fin spines, and the one which differentiates them from all other species of *Hybodus*, is that the enamel ridges on the distal part of the spine are very short, ending at or above the level of the lowermost denticles on the posterior face of the spine, and well above the apex of the groove on the posterior face of the proximal part of the spine which housed the basal cartilage of the fin. The trivial name of the species refers to these short ribs on the fin spine.

The spines are not strongly arched, the anterior edge curving through about 35°, the posterior through 25°, and are strongly compressed. The anterior edge is keeled and there is a well marked angle between the lateral and posterior faces. On the lateral face the ridges of enamel are well spaced. In both specimens a median

enamel ridge forms the keel on the anterior edge. In the Henfield spine (?posterior) there are ten ridges on each side, five reaching the tip of the spine and five being confined to the proximal part. In the Isle of Wight spine there are eleven ridges on each side, seven of which extend to the tip. In the Henfield spine all the ridges end above the level of the lowermost denticle on the posterior face, the longest ribs being the first and second on the right side and the third on the left side. In the Isle of Wight spine the longest ridges are the first on each side, and they alone extend beyond the level of the lowest denticle on the posterior face.

The denticles on the posterior face of the spine are in a single median series. This single series is clearly the result of unequal development of paired denticles, for occasionally the denticles are double (Pl. 3, figs. 1*a*, 2*a*), and in other cases at the base of a fully developed denticle there is the rudiment of a second. The side on which these rudimentary denticles occurs is variable, showing that the single series of denticles is not the result of suppression of either the left or right series of denticles, but of apparently random suppression of one of each pair. In the Isle of Wight spine, which is complete to the tip, there is a total of 27 denticles, of which two show doubling and eight show rudiments of a second denticle, six on the right side and two on the left of a fully developed denticle. In the Henfield spine sixteen denticles are preserved, one is doubled, and one has a rudiment on its left side. The denticles are very variable in shape : some are strongly hooked, either to the left or the right, some are straight, and while the majority are smooth, some, particularly towards the base of the spine, bear striae like those on the teeth.

Lack of material at present prevents the preparation of thin sections of the spines, but broken surfaces show that in structure the spine agrees with *H. aschersoni* Stromer (1927 : 20, pl. 3, fig. 9, text-fig. 13) from the Cenomanian of Libya, in that in the exserted part of the spine the pulp cavity is surrounded by a zone of lamellar tissue which makes up about half the thickness of the wall of the spine, the outer part of the wall consisting of osteodentine. Passing back towards the base of the spine the zone of lamellar tissue becomes thinner until it disappears below the apex of the groove in the hind edge of the spine. Below this level the spine consists of osteodentine alone.

Affinities. Teeth of *H. brevicostatus* from horizons below the Weald Clay suggest that in the history of the species between the Ashdown Beds and the Weald Clay there was an increase in size accompanied by an increase in the number of striae on the crown and in the number of accessory cusps. Small teeth from the Weald Clay of Henfield show that in the ontogeny of the species increase in size was accompanied by increase in the number of striae on the crown and reduction in the individuality of the lateral cusps. Both these facts suggest that the ancestor of *H. brevicostatus* was a rather small, low-crowned species, extant during or before the deposition of the Ashdown Beds, with sparse, coarse striae on the crown, three or four pairs of lateral cusps and a tendency to develop accessory cusps. These conditions are met by *H. parvidens*, and it seems very probable that *H. brevicostatus* is an offshoot of this species, probably originating near the base of the Wealden.

The increase in ornamentation and reduction in the individuality of the lateral

cusps which occur with increased size is an interesting feature of this species. In the holotype it results in some of the teeth, especially the more posterior ones, having a very *Acrodus*-like crown, sometimes without distinguishable lateral cusps or with very numerous small ones. These conditions are just those found in some Upper Cretaceous species such as *Synechodus illingworthi* (Dixon) (Smith Woodward 1911 : 220, pl. 46, figs. 5–7) from the Cenomanian zones of the English Chalk; *Hybodus brabanticus* Leriche (1929 : 225, text-figs. 4, 5; 1930 : 105) and *Acrodus dolloi* Leriche (1929 : 228, text-figs. 6, 7) from the Lower Senonian of Belgium; *Hybodus grewingki* Dalinkevičius (1935 : 256, pl. 1, figs. 36–38) and *Acrodus guedroyii* Dalinkevičius (1935 : 256, pl. 1, figs. 34, 35) from the Cenomanian of Lithuania; *Acrodus affinis* Reuss (1845 : 1, pl. 2, figs. 3, 4), *Hybodus bronnii* Reuss (1845 : 97, pl. 24, fig. 26, pl. 42, fig. 7) and *Hybodus cristatus* Reuss (1845 : 2, pl. 2, fig. 20), all from the Turonian Plänerkalk of Bohemia; and the teeth from the Upper Sononian of Aachen, Germany, described as *Hybodus* ? sp. and *Acrodus* ? sp. by Albers & Weiler (1964 : 4, 5, text-figs. 3, 8, 9, 42). These species are also the only marine hybodonts known by teeth in the Upper Cretaceous. The best known of them is *Acrodus illingworthi* Dixon, a species transferred to the heterodontid genus *Synechodus* by Smith Woodward (1891 : 66). But there is no real evidence that this species is not a hybodont: all the teeth have typical hybodontoid roots, without the development of enlarged central foramina which is characteristic of *Synechodus* and other heterodontids (Casier 1947*b* : 2). The absence of hybodont fin spines in the English Chalk is not evidence against the species being hybodont, for only about twenty teeth are known, and judging by the conditions in *H. brevicostatus* an individual would produce well over two hundred teeth in its life but only two spines. It is also quite possible that these Upper Cretaceous hybodonts should have lost their fin spines. The syntypes and other material of *A. illingworthi* in the British Museum (Natural History) show a strong resemblance to *H. brevicostatus*, and with Leriche (1929 : 227) I believe the species should be named *Hybodus illingworthi* (Dixon). *H. brabanticus* Leriche is almost certainly a synonym of *H. illingworthi*, for Leriche included in his species some specimens figured by Smith Woodward (1911, pl. 46, fig. 7) as *S. illingworthi*, but these teeth (43511) occur in association with other teeth which are undoubtedly *H. illingworthi*. There seems little to distinguish *H. grewingki* Dalinkevičius from *H. illingworthi*, and Dalinkevičius noted the resemblance between his material and Leriche's *H. brabanticus*. Reuss's species from the Turonian of Bohemia are large teeth of the same type as *H. illingworthi* and *H. brevicostatus*. The Upper Senonian *Hybodus* teeth described by Albers & Weiler are compared by them with *H. illingworthi* and *H. brabanticus*, which they closely resemble. *Acrodus dolloi* Leriche and *A. guedroyii* Dalinkevičius are based on large teeth which resemble Lower Lias species such as *A. curtus* (=*A. anningiae*) and *A. nobilis*; the *Acrodus* teeth described by Albers & Weiler are very like *A. dolloi* but smaller. There is no other evidence of *Acrodus* of this type in the Cretaceous, but these teeth, in size, shape and ornamentation, bear considerable resemblance to the large postero-lateral teeth of *H. brevicostatus*, and could be derived from this species by further increase in size, in the number of striae and in the loss of individuality of the lateral cusps.

Fin Spines of Hybodus

Only in *H. basanus* and *H. brevicostatus* among Wealden and Purbeck sharks have fin spines been found in association with teeth. Smith Woodward (1916) suggested relationships between the various spines and teeth known from the British Wealden and Purbeck. His conclusions may be summarized as follows :

Tooth	Horizons	Spine
H. basanus	Weald Clay	? *H. sulcatus* Agassiz
' teeth of the same general type as *H. basanus* '	Wadhurst Clay Grinstead Clay	*H. subcarinatus* Agassiz
H. ensis	Middle Purbeck	' almost identical with *H. dorsalis* Agassiz '
H. parvidens	Wadhurst Clay	?
?	Grinstead Clay	*H. striatulus* Agassiz
?	Middle Purbeck	*H. strictus* Agassiz

Of the spines which Smith Woodward did not associate with species based on teeth, he compared *H. striatulus* with the Purbeck spines assigned to *H. ensis*, and *H. strictus* with *H. subcarinatus* and *H. basanus*.

We now have more complete information on the ranges and relationships of the Wealden and Purbeck teeth of *Hybodus*. *H. parvidens* is a species which ranged from the Middle Purbeck to the Weald Clay, giving rise to *H. basanus* in the Weald Clay, the evolution of *H. basanus* involving an increase in size of the teeth. We should therefore expect the fin spines of *H. parvidens* to be similar to those of *H. basanus* but smaller, and to range from the Middle Purbeck to the Lower Weald Clay. These conditions are met by *H. strictus* Agassiz in the Purbeck (12–13 cm. long) and *H. subcarinatus* Agassiz in the Wadhurst and Grinstead Clay (14–17 cm. long).

The ' teeth of the same general type as *H. basanus* ' with which Smith Woodward associated *H. subcarinatus* Agassiz are shown above (p. 294) to belong in *H. ensis* : one would therefore expect them to be associated with spines of the same type as *H. dorsalis* Agassiz—this condition is met by *H. striatulus* Agassiz.

A revised scheme of the (hypothetical) relationships between hybodont teeth and fin spines in the Wealden and Purbeck is as follows :

Tooth	Horizons	Spine
H. ensis	Middle Purbeck– Grinstead Clay	cf. *H. dorsalis* (Purbeck) *H. striatulus* (Wealden)
H. parvidens	Middle Purbeck– Weald Clay	*H. strictus* (Purbeck) *H. subcarinatus* (Wealden)
H. basanus	Weald Clay	? *H. sulcatus*
H. brevicostatus	Ashdown Beds–Weald Clay	*H. brevicostatus*

In the Wealden and Purbeck there occur tuberculated fin spines which have been described as *Asteracanthus* (*A. verrucosus* Egerton 1854, Middle Purbeck, Swanage ; *A. semiverrucosus* Egerton 1854, Middle Purbeck, Swanage ; *A. granulosus* Egerton, 1854, Wealden, Sussex). A spine from the Lower Neocomian of the Paris Basin is described as *A.* cf. *acutus* Agassiz by Leriche (1911 : 456, pl. 6, fig. 1), and *A. granulosus* has also been recorded from the Lower Neocomian of Switzerland, where it occurs

in the same beds as teeth of '*Strophodus*' (=*Asteracanthus*) which according to Peyer (1946 : 54) are not derived fossils. But although *Asteracanthus* occurs in the marine Lower Cretaceous, it seems very unlikely that the British spines are true *Asteracanthus*—that is, that they are from a fish with '*Strophodus*' teeth, like the better known Jurassic species, for the large and conspicuous teeth could hardly have escaped notice, particularly since about a dozen spines of this type are known and in any individual there will be at least fifty teeth to each spine. The preservation of the spines is such that they can hardly be derived from older formations. The answer is probably that these spines are *Hybodus* in which the normal enamel ridges have broken up into separate tubercles as a stage in the reduction of the spine. This argument is supported by the presence of normal ridges on the distal (and first formed) parts of the spines, by the Wealden *H. striatulus* Agassiz (suggested above to belong to *H. ensis*) where the ridges are partially broken up into tubercles, and by the tendency in many Wealden *Hybodus* spines for the ridges to become fragmented proximally.

Remarks on Hybodont Teeth

This study has shown that where abundant isolated teeth of *Hybodus* from successive horizons are available, the distinctions between species become very difficult to maintain. A great deal of parallelism and convergence is bound to occur in the evolution of sharks' teeth, and further uncertainty arises from the degree of heterodonty of species (usually unknown) and from variability within a species. It is clear that the erection of new species of hybodont sharks on one or two isolated teeth is an extremely hazardous procedure.

The changes which occur in the teeth of Wealden hybodont sharks from species to species and horizon to horizon allow one to draw some general conclusions about the correlation between various dental characters in hybodonts. These can be summarized as follows :

(*a*) Characters which increase with increasing height of crown and decrease with decreasing height of crown.

1. lingual curvature of crown
2. compression of crown
3. lingual curvature of root
4. difference between ornament on labial and lingual faces of crown.

(*b*) Characters which decrease with increasing height of crown and increase with decreasing height of crown.

1. degree of heterodonty
2. number of lateral cusps
3. number and size of accessory cusps
4. depth of root
5. height of striae on crown
6. bifurcation of and anastomosis between striae

(*c*) Characters which increase with increasing size of tooth.

1. number of striae on crown.

This list of characters showing correlation with the height of the crown or the size of the tooth includes almost all those commonly used to distinguish hybodont species. If all these characters are correlated with an obviously adaptive feature like crown height it is clear that it will often be impossible to distinguish on teeth alone between relationship, parallelism and convergence. There is therefore little likelihood of any worthwhile subdivision of the genus *Hybodus*, now so large both in number of species and in range, on characters of the dentition. Jaekel's (1889, 1898) attempt at a subdivision was largely based on features of the teeth which are obviously adaptive or are correlated with adaptive features : of the four genera which he proposed, only *Polyacrodus*, distinct on histological characters (thickness of pallial dentine), has been generally accepted.

We are forced to look for other characters on which species of *Hybodus* may be grouped, but if the earliest (Lower Lias—*H. delabechei* etc.) and latest (Upper Wealden —*H. basanus*) species in which the anatomy is well known are compared, the only differences seem to be reduction of the cephalic spines (present in males only) from two pairs to one, the appearance of symphysial teeth, and slight changes in the fin spines (increase in thickness of the lamellar tissue, reduction in the strength of the enamel ridges, reduction in the distance between the paired denticles on the hind edge, culminating in suppression of one of each pair in *H. brevicostatus*). The first two of these differences are suitable for generic subdivision, but until their distribution is known in many more species no useful purpose is served by such division.

Genus ***LONCHIDION*** Estes 1964 : 7

Amended diagnosis. Small fresh-water hybodonts, weakly or strongly heterodont, known only by isolated teeth, cephalic spines and fin spines. Teeth low-crowned, elongated, crown not much deeper than root ; tricuspid anterior teeth present in some forms ; crown smooth or with sparse vertical striae, large labial projection or buttress below central cusp, lateral cusps absent or small and irregular ; root hybodontoid except in supposed tricuspid anterior teeth of advanced forms, where it is squatinoid ; pallial dentine of crown very thick, as in *Polyacrodus*. Fin spines with or without enamel ridges on lateral faces, with a single series of posterior denticles. Cephalic spines of normal hybodont type, without terminal barb.

Type species. *Lonchidion selachos* Estes (1964 : 7, text-figs. 1–4), Lance Formation, Wyoming.

Lonchidion breve sp. nov.

(Pl. 5, fig. 3 ; Text-figs. 14–20, 29E)

Diagnosis. *Lonchidion* known only by isolated teeth, 3·5 mm. or less in length ; no tricuspid anterior teeth, dentition weakly heterodont ; crowns of teeth rather short, with maximum breadth between half and one-quarter of the length ; crown smooth or very feebly striated, lateral and accessory cusps very small and irregular when present, labial process strong.

HOLOTYPE. P.47024 (Text-fig. 14), complete tooth from the Paddockhurst bone-bed (Grinstead Clay); Sussex.

MATERIAL. About one hundred and sixty teeth, mostly without roots.

HORIZONS AND LOCALITIES. Ashdown Beds: Cliff End bone-bed, Cliff End, Sussex. Wadhurst Clay: Telham bone-bed, Stone, Kent; top of cliff near Hastings harbour, Sussex; Ashurstwood, Sussex. Grinstead Clay: Paddockhurst bone-bed, Sussex. Weald Clay: Henfield, Sussex. Atherfield Clay: *Perna* Bed, Sandown Bay, Isle of Wight (probably derived from Wealden Shales—see p. 319).

The teeth which are assigned to this species fall into three types which intergrade both morphologically and stratigraphically: they will be described separately as three subspecies.

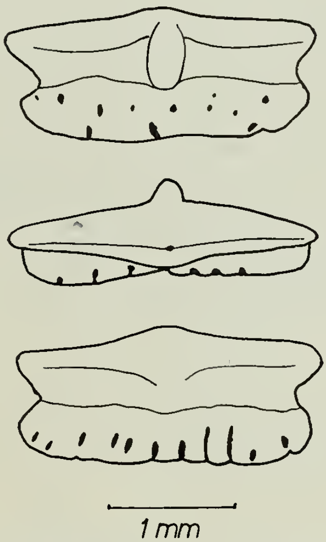


FIG. 14. *Lonchidion breve breve* sp. et ssp. nov. P.47024, the holotype, a lateral tooth in labial (above), occlusal (centre) and lingual view. Grinstead Clay, Paddockhurst Bone-bed; Paddockhurst Park, Sussex.

Lonchidion breve breve sp. et ssp. nov.

(Pl. 5, fig. 3; Text-figs. 14–16, 29E)

DIAGNOSIS. *Lonchidion breve* in which the crown of the tooth is normally smooth, without lateral or accessory cusps or striations.

HOLOTYPE. P.47024, complete tooth (Text-fig. 14) from the Paddockhurst bone-bed.

MATERIAL In addition to the holotype, about 120 teeth, mostly without roots.

HORIZONS AND LOCALITIES. Ashdown Beds: Cliff End bone-bed. Wadhurst Clay: Telham bone-bed, Stone, Kent; Hastings, Sussex; Ashurstwood, Sussex.

Grinstead Clay: Paddockhurst bone-bed. Weald Clay: Henfield. Atherfield Clay: *Perna* Bed, Sandown Bay, Isle of Wight.

DESCRIPTION. This subspecies, the typical and commonest form of the species, occurs throughout the Wealden. In the majority of specimens only the crown is preserved, and in many examples, especially those from the Cliff End and Paddockhurst bone-beds, the teeth have undergone a good deal of *post mortem* abrasion. None of the teeth exceeds 3·5 mm. in length. The crown is normally completely smooth, without ornament or any indication of lateral cusps. There is a single, very low cusp which lies at or near the centre of the crown. The occlusal edge of the tooth is compressed into a more or less sharp ridge. Below the central cusp there is a strong rounded process or buttress on the labial face of the crown. The root plays no part in the formation of this process, and is overhung by it. A ridge normally runs on to the labial process from the central cusp. On the lingual face of the crown there is a gentle swelling opposite the central cusp and the labial process. The occlusal surface of the crown is much longer than its base, so that the tooth is strongly waisted at the junction of root and crown.

The root is preserved in few specimens, and is always somewhat worn. It is typically hybodontoid (Casier 1947*a* : 9), with no specialized vascular foramina. On the lingual face of the root there is a row of vertically elongated foramina and on the labial face irregularly scattered foramina (Text-fig. 14). The root is almost as deep as the crown and only slightly shorter.

In the type species of *Lonchidion*, the Late Cretaceous *L. selachos* Estes (see p. 330),

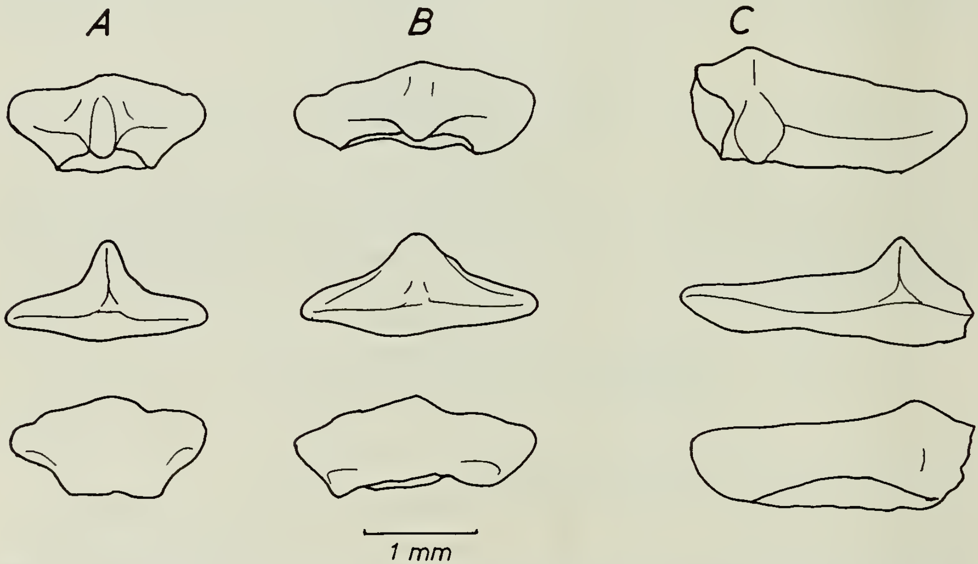


FIG. 15. *Lonchidion breve breve* sp. et ssp. nov. Three teeth from the Ashdown Beds, Cliff End Bone-bed; Cliff End, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.46993; B. P.46995; C. P.47005.

the histological structure of the crown is described (Estes 1964 : 8, text-fig. 2D) as a fan-shaped radiation of dentine tubules from one central cavity which originated along a central longitudinal axis. The tooth crowns of *L. breve breve* (Pl. 5, fig. 3; Text-fig. 29E) agree with this description. Below a rather thick layer of enamel the crown is made up of pallial dentine containing long, subparallel, much branched tubules which arise from the tips of vascular canals which end shortly after entering the centre of the base of the crown. Estes compares this structure with that seen in teeth of the Triassic hybodont *Palaeobates* (Jaekel 1889, pl. 10, fig. 2; Seilacher 1943, text-figs. 22, 29, 34), especially with *P. nodosus* Seilacher. But in *Palaeobates* (Pl. 5, fig. 2) the dentine tubules are longer, parallel and more regularly branched than they are in *Lonchidion*, and they arise not from the tips of vascular canals but from a single open pulp cavity running the length of the tooth. The pallial dentine of *Lonchidion* is much more like that in the Triassic *Polyacrodus*, particularly in small species like *P. minimus* (Seilacher 1943, text-figs. 7–10; Pl. 5 fig. 1), where there are just the same wavy, irregularly branched dentine tubules arising from short vascular canals near the base of the crown. In *Polyacrodus* the pallial dentine is a little thinner than it is in *Lonchidion*, perhaps because of the greater size of the teeth, but in other respects the correspondence is exact.

The worn condition and absence of roots in most examples of this sub-species make it difficult to arrive at any clear idea of the variation in shape. The length of the crown ranges from 1·4–3·4 mm., the maximum breadth of the crown (at the labial process) from 0·4–1·2 mm. In five complete teeth the depth ranges from 1·0–1·35 mm., the ratio of depth to length from 1·5–2·5. The crown is normally broader than deep, the ratio of maximum breadth to length ranging from 1·9–3·8, and of maximum depth to length from 2·7–4·2. The shorter, deeper teeth, in which the labial process is large (Text-figs. 15A, 16A) are probably anterior; longer teeth, still with a strong labial process (Text-fig. 15B), antero-lateral; the longest teeth

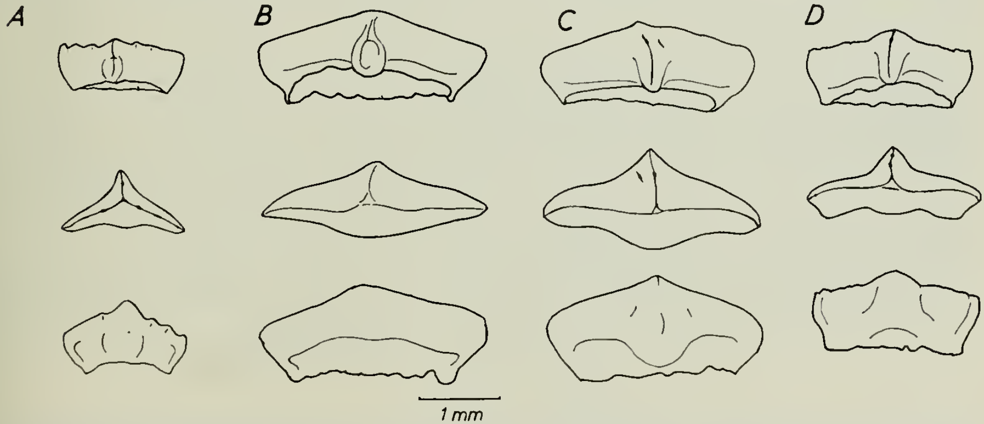


Fig. 16. *Lonchidion breve breve* sp. et ssp. nov. Teeth in labial (above), occlusal (centre) and lingual view. A, B. P.47324, P.47047 from the Weald Clay of Henfield, Sussex. C, D. P.39015, P.39011 from the *Perna* Bed, Atherfield Clay; Sandown Bay, Isle of Wight.

(Text-figs. 14, 15C) lateral, and shallow teeth with a weak labial process are probably posterior (Text-fig. 16B).

At lower horizons there is no difficulty in distinguishing between *L. breve breve* and the other subspecies of the species, but at higher horizons, the Weald Clay of Henfield and the *Perna* Bed in the Atherfield Clay, examples occur in which there are weak accessory cusps (Text-fig. 16C) or lateral cusps (Text-fig. 16A, D). These specimens tend towards *L. breve pustulatum*, to which most of the *Perna* Bed teeth belong, and also towards *L. selachos* Estes, from the Upper Cretaceous of America (see p. 330).

Lonchidion breve crenulatum sp. et ssp. nov.

(Text-figs. 17, 18)

Diagnosis. *Lonchidion breve* in which the occlusal margin of the tooth crown is irregularly crenulate, and in which the lingual and labial faces of the crown are weakly and sparsely striated.

Holotype. P.47060 (Text-fig. 17B), tooth without root from the Paddockhurst bone-bed.

Material. In addition to the holotype, twenty-five teeth, all without roots.

Horizons and localities. Wadhurst Clay: Ashurstwood, Sussex. Grinstead Clay: Paddockhurst bone-bed.

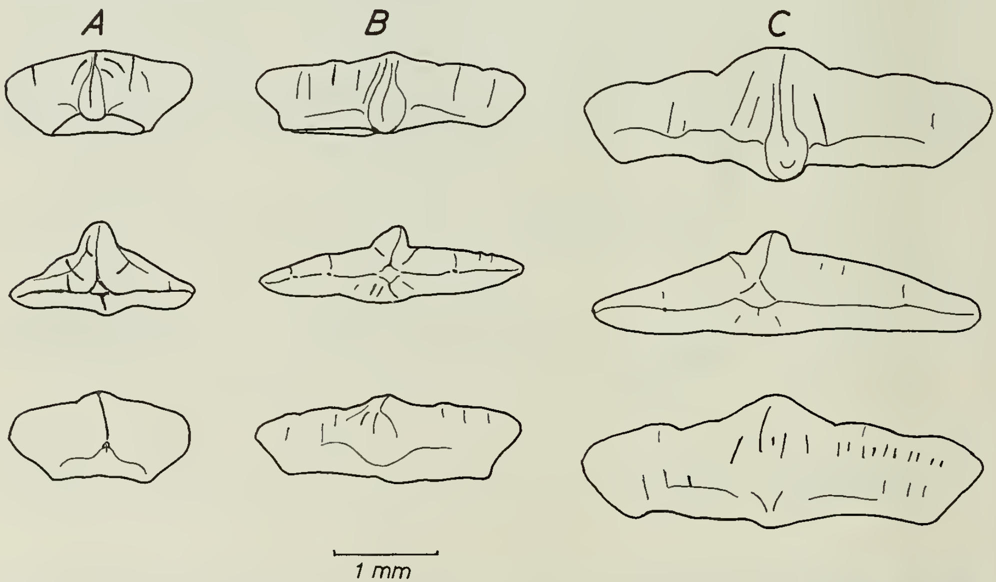


Fig. 17. *Lonchidion breve crenulatum* sp. et ssp. nov. Three teeth from the Grinstead Clay, Paddockhurst Bone-bed; Paddockhurst Park, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47059. B. P.47060, the holotype. C. P.47066.

Description. In this subspecies the form and proportions of the teeth do not differ significantly from those in *L. breve breve*. The largest tooth (Text-fig. 17C) is 3·5 mm. long, similar in size to the largest *L. breve breve*. The occlusal crest of the teeth is produced into a number of small and irregular lateral cusps or beads. Both the lingual and labial faces of the crown bear a number of weak, parallel, vertical striae, the striae being strongest at the central cusp. Both the beading of the occlusal crest and the striation of the crown are weakest in the short, deep anterior teeth (Text-fig. 17A), strongest in the longer, lower lateral and posterior teeth.

Remarks. This subspecies is commonest in the Paddockhurst bone-bed, where it accounts for about half of the specimens of *Lonchidion breve*, the other half being *L. breve breve*. The fact that teeth of *L. b. crenulatum* from this horizon exhibit the same range of size and shape as those of *L. b. breve* (cf. Text-figs. 15, 17) and the ab-

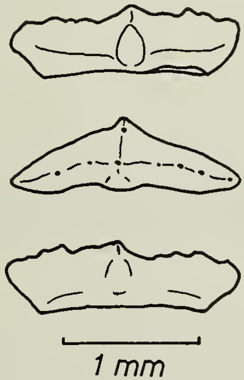


Fig. 18. *Lonchidion breve crenulatum* sp. et ssp. nov. P.47081, a tooth from the Wadhurst Clay; Ashurstwood, Sussex, in labial (above), occlusal (centre) and lingual view.

sence of *L. b. crenulatum* at Cliff End and in the Telham bone-bed show that the two subspecies are distinct forms, not teeth from different parts of the mouth of the same fish. *L. b. crenulatum* is not known above the Grinstead Clay. In a sample of four teeth of *Lonchidion* from the Wadhurst Clay at Ashurstwood, Sussex, three are *L. b. crenulatum* (Text-fig. 18) and one is *L. b. breve*. *L. b. crenulatum* does not occur in the large sample of *Lonchidion* from the Cliff End bone-bed in the Ashdown Beds or the Telham bone-bed at the base of the Wadhurst Clay, nor is it known in the Purbeck, although the posterior teeth of *L. heterodon* (Text-fig. 25C) are very like it. In spite of this resemblance, it seems probable that *L. b. crenulatum* is a subspecies which evolved from *L. b. breve*, probably early in Wadhurst Clay time.

Lonchidion breve pustulatum sp. et ssp. nov.

(Text-fig. 19)

Diagnosis. *Lonchidion breve* in which the occlusal crest of the crown is weakly, irregularly and finely crenulate, and in which the labial face of the crown bears a number of minute accessory cusps but no striations.

Holotype. P.47085, (Text-fig. 19B), tooth without root from the *Perna* Bed, Atherfield Clay, Sandown Bay, Isle of Wight (? derived from the Wealden Shales—see below).

Material. In addition to the holotype, fourteen teeth, all without roots.

Horizon and locality. *Perna* Bed, Atherfield Clay: Sandown Bay, Isle of Wight.

Description. In this subspecies the form and proportions are again very similar to those in *L. breve breve*. The teeth range in length from 1·8–3·6 mm., in breadth from 0·6–1·3 mm., and in the ratio of breadth to length from 2·0–3·6. The occlusal

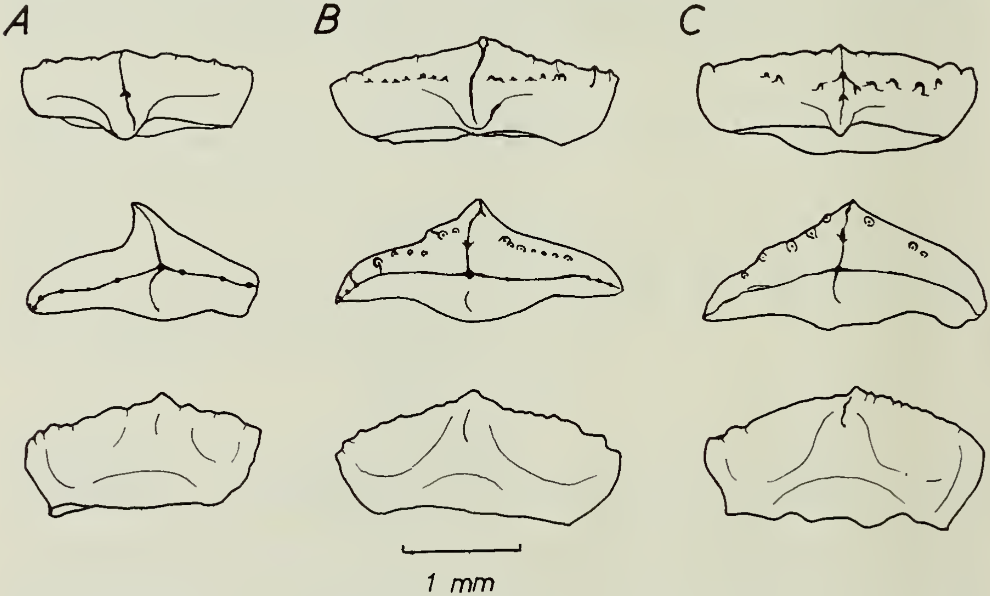


Fig. 19. *Lonchidion breve pustulatum* sp. et ssp. nov. Teeth from the *Perna* Bed, Atherfield Clay; Sandown Bay, Isle of Wight, in labial (above), occlusal (centre) and lingual view. a. P.47088. b. P.47085, the holotype. c. P.47089.

crest of the teeth is produced into irregular lateral cusps or beads, and these are more numerous than they are in *L. breve crenulatum*. The labial and lingual faces of the crown are without striae. The labial process, below the central cusp, is not so well marked off from the body of the crown as it is in the other subspecies (Text-fig. 19B, C), and the ridge on its occlusal surface bears one or sometimes two small cusps. Level with the more labially placed of these cusps on the labial process there is a series of very small accessory cusps on the labial surface of the crown, which extends as a shallow shelf at this level. The strength and number of these accessory cusps seem to be correlated with the breadth of the tooth (Text-fig. 19), but not with its length, and no real distinction between anterior and posterior or lateral teeth can be made.

REMARKS. This subspecies is known only in the *Perna* Bed, at the base of the Lower Greensand. Most of the fish teeth from this horizon are derived from the underlying Wealden Shales (Casey 1961 : 505), and this is probably true of the specimens of *Lonchidion*, a genus otherwise unknown in marine beds. The teeth are not much rolled or waterworn, but their small size will probably account for this. Together with *L. b. pustulatum* in the *Perna* Bed there occur teeth which are referred to *L. b. breve* but which show faint traces of the lateral and accessory cusps which characterize *L. b. pustulatum* (Text-fig. 16C, D) : Similar examples also occur at Henfield (Text-fig. 16A). These forms leave little doubt that *L. b. pustulatum* has evolved directly from *L. b. breve* by extension of the labial face of the crown into a shelf bearing accessory cusps. Teeth of *L. b. pustulatum* are very like the smallest posterior teeth of the ptychodont genus *Hylaeobatis*, suggesting a possible relationship which is discussed on p. 341.

The Arrangement of the Teeth

Many of the teeth of *Lonchidion breve* have a strong wear facet on the occlusal margin of the crown, the occlusal crest and central cusp being planed off into a level surface. This indicates, as one would deduce from the form of the teeth, that *L. breve* was a durophagous form, grinding its food by rubbing the upper and lower teeth across one another. In many specimens of *L. breve* there is also a vertical groove or scar in the centre of the lingual face of the crown : this is a pressure scar formed by the tip of the labial process of the succeeding tooth, which shows that successive teeth in each file were in contact or nearly so. If the tip of the labial process of each tooth touched the centre of the lingual face of the crown of the preceding tooth, there would be a space between the tapering lateral parts of the teeth—such spaces are disadvantageous in durophagous forms, and they must have been filled by the lateral parts of the teeth of the adjacent file (Text-fig. 20). It follows that in *L. breve* there was overlap between the files of teeth, and that there must therefore have been regular alternation between the teeth in adjacent files : this is an advanced character recalling the rays, which does not normally occur in hybodonts

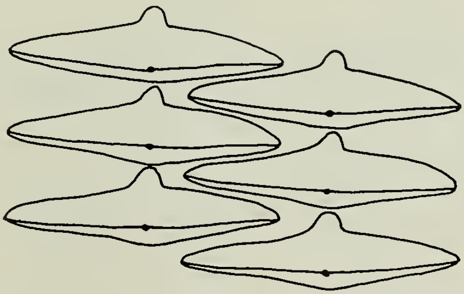


FIG. 20. *Lonchidion breve* sp. nov. Diagram showing the probable arrangement of adjacent files of teeth in occlusal view, ×15. Based on the holotype (Text-fig. 14).

and heterodontids (Casier 1953 : 40), although it is present in the Triassic fresh-water form *Lissodus africanus* (Brough 1935, pl. 2, figs. 2, 3), at least in the anterior and lateral parts of the jaw.

Lonchidion striatum sp. nov.

(Text-figs. 21, 22)

DIAGNOSIS. *Lonchidion* known only by isolated teeth, 4·5 mm. or less in length ; no tricuspid anterior teeth, dentition weakly heterodont ; crowns of teeth elongated, maximum breadth rarely less than one-quarter of the length ; occlusal crest of teeth strong, lateral cusps very weak and irregular ; both labial and lingual faces of crown with strong vertical striae, occasionally bifurcated basally, which diverge from the occlusal crest but do not reach the base of the crown ; labial process small and weak.

HOLOTYPE. P.47103 (Text-fig. 21C), a complete tooth from the Weald Clay of Henfield, Sussex.

MATERIAL. In addition to the holotype, one hundred teeth, of which nine are complete.

HORIZON AND LOCALITY. Weald Clay : Henfield, Sussex.

DESCRIPTION. The teeth of this species from Henfield are all well preserved, with little or no wear, but the root is present in only nine of the one hundred examples. The teeth range in length from 1·1 to 4·2 mm. In shape and proportions the teeth are similar to those of *L. breve breve* and *L. b. crenulatum* except that they are more elongated. Only in two teeth out of fifty does the ratio of maximum breadth to length of the crown fall below 4·0, the mean ratio being 5·9 (compared with about 2·7 in *L. b. breve*). The longitudinal occlusal crest of the crown is strongly marked,

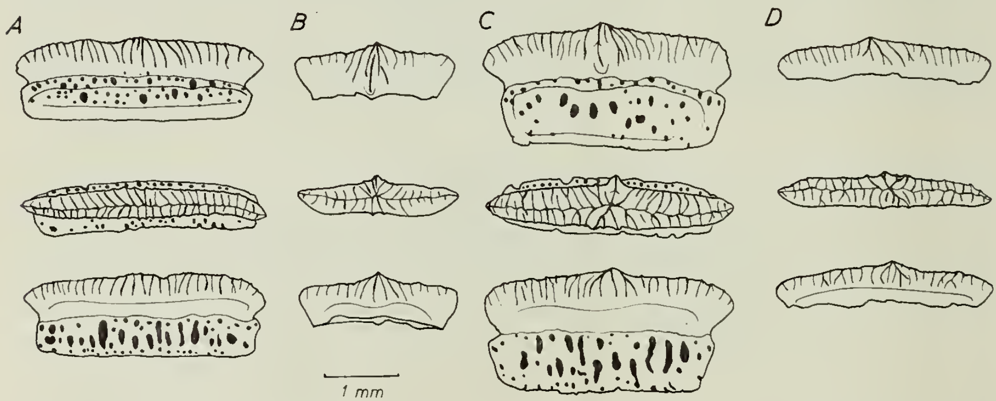


FIG. 21. *Lonchidion striatum* sp. nov. Teeth from the Weald Clay of Henfield, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47094. B. P.47095. C. P.47103, the holotype. D. P.47106.

and there is a low central cusp. The occlusal crest is roughened and jagged, as in *L. b. crenulatum*, but distinct lateral cusps are not recognizable. Diverging from the occlusal crest there are well marked vertical striae on both labial and lingual faces of the crown, the striae being stronger and more numerous than in *L. b. crenulatum*. The striae are occasionally bifurcated basally, especially at the central cusp, where they are longest and strongest. The striae do not reach the base of the crown. The labial process is weaker than in *L. breve*, particularly in the more elongated teeth, where it may almost disappear (Text-fig. 21A). The striae are weakest in the smaller and shorter teeth (Text-fig. 22A).

The root is about as deep as the crown, and is hybodontoid, without specialized foramina, just as in *L. breve*. In histological structure the crown agrees with that of *L. breve* in being made up almost entirely of pallial dentine.

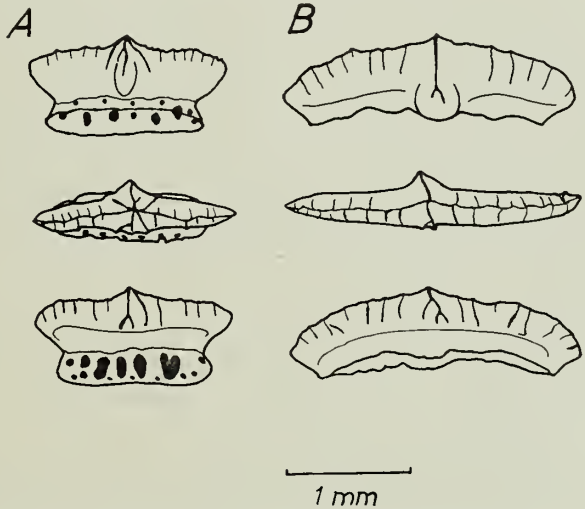


FIG. 22. *Lonchidion striatum* sp. nov. Teeth from the Weald Clay of Henfield, Sussex, in labial (above), occlusal (centre) and lingual view. A. P.47130. B. P.47138.

There is little variation in the shape of the teeth, and the dentition must have been weakly heterodont. The shorter, broader teeth, with the weakest striae (Text-figs. 21B, 22A), are probably anterior, longer teeth (Text-figs. 21C, 22B) lateral, and long, slender teeth, with a very small labial process (Text-fig. 21A, D), posterior, similar variations being evident in *L. breve crenulatum* (Text-fig. 17).

AFFINITIES. *Lonchidion striatum* differs from *L. breve crenulatum* only in the greater length of the teeth (ratio of breadth to length usually well over 4·0, always less than 4·0 in *L. b. crenulatum*), stronger and more numerous striae, and weaker labial process. There can be little doubt that *L. striatum*, known only in the Weald Clay, has evolved directly from *L. breve crenulatum*, which is unknown above the Grinstead Clay, by elongation of the teeth and strengthening of the surface ornament. The reduction of the labial process in the lateral and posterior teeth of *L. striatum*

means that there would be little space between the lateral parts of successive teeth (cf. Text-fig. 20) and little or no overlap between adjacent files of teeth, producing a more *Hybodus*-like dentition than in *L. breve*.

In shape, teeth of *L. striatum* are similar to some of the Triassic species of *Acrodus* and *Polyacrodus* such as the Spitzbergen species *Polyacrodus pyramidalis* Stensiö (1921, pl. 2, figs. 21–26), *Acrodus spitzbergensis* Hulke (Stensiö 1921, pl. 2, figs. 1–19), *A. vermiformis* Stensiö (1921, pl. 2, figs. 20, 21) and *A. oppenheimeri* Stensiö (1921, pl. 3, figs. 1–11) though the teeth of all these species are larger than those of *L. striatum*.

Lonchidion rhizion sp. nov.

(Text-figs. 23, 24)

DIAGNOSIS. *Lonchidion* known only by isolated teeth less than 2 mm. in length ; no tricuspid anterior teeth, dentition strongly heterodont ; crowns of teeth very short and broad, maximum breadth more than half of the length ; occlusal surface of teeth formed entirely by labial surface of crown and of labial process, which is much enlarged and probably overlapped the crown of preceding tooth ; crown smooth, without ornament or lateral cusps ; lingual surface of crown with pair of depressions or sockets separated by central crest which probably articulated with pulp cavity of succeeding tooth ; pulp cavity small, root absent or very small.

HOLOTYPE. P.47144, tooth without root (Text-fig. 23B), Cliff End bone-bed, Cliff End, Sussex.

MATERIAL. In addition to the holotype, thirty-five teeth, all without roots.

HORIZONS AND LOCALITIES. Ashdown Beds : Cliff End bone-bed, Cliff End, Sussex, (25 teeth). Wadhurst Clay: Telham bone-bed, Stone, Kent (5 teeth). Grinstead Clay : Paddockhurst bone-bed, Paddockhurst Park, Sussex (5 teeth).

DESCRIPTION. The teeth assigned to this species vary from examples which do not differ much from *L. breve breve* (Text-fig. 23A) to extremely specialized types which

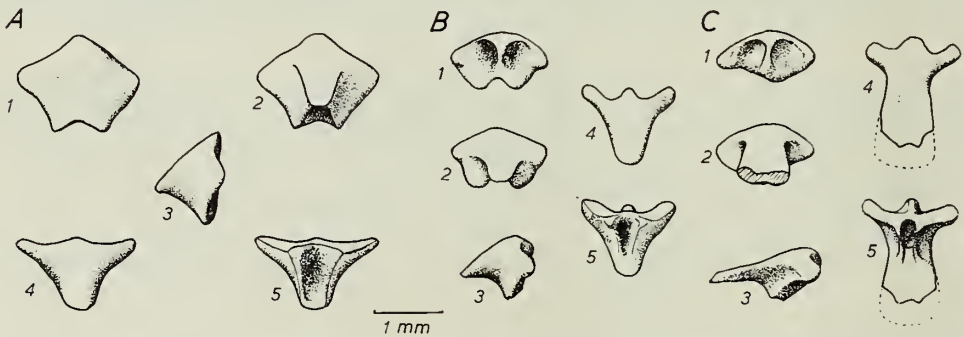


FIG. 23. *Lonchidion rhizion* sp. nov. Teeth from the Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex, in lingual (1), labial (2), medial (3), occlusal (4) and basal (5) view. A. ? anterior tooth P.47143. B. ? lateral tooth, P.47144, the holotype. C. ? posterior tooth, P.47150.

would hardly be interpreted as sharks' teeth were they not linked by intermediate forms with the more recognizable specimens. All the teeth are very small, ranging in length from 1·0 to 1·9 mm., and they are broad and deep ; the ratio of maximum breadth to length ranges from 0·75 to 2·0, that of depth to length from 1·0 to 2·4.

The deeper, narrower teeth (Text-fig. 23A) are similar to the (presumed) anterior teeth of *L. breve breve* (Text-fig. 15A). In these teeth the crown is almost as deep as long, and is deeper than broad. The crown is pentagonal in lingual and labial view, two sides of the pentagon forming the occlusal crest and meeting in a rounded central cusp, two sides sloping inwards towards the base, and one side forming the base. The lingual face of the crown is almost smooth, with a slight swelling below the central cusp and a shallow depression on each side of this. In occlusal view the crown is triangular, the longest side being the occlusal crest and the apex the labial process. The labial process is much broader than it is in *L. breve*, and its flat upper surface merges with the upper part of the labial face of the crown to form the smooth, sloping occlusal surface of the tooth. There is no ridge running on to the labial process from the central cusp as there is in *L. breve*. The underside of the labial process is hollowed out, this hollow being continuous basally with the small pulp cavity of the crown.

More specialized, but linked by intermediate forms with the teeth described above, are teeth of the type shown in Text-fig. 23B. In these the crown is shallower but broader, and is almost as broad as long. The lingual face of these forms bears a central vertical crest with a well marked, circular depression on each side of it. The occlusal margin of the crown is lower and more gently rounded, the central cusp hardly recognizable in labial or lingual view but showing in occlusal view as a knob at the top of the central crest on the lingual surface. The labial process is longer than in the forms described above, and the occlusal surface formed by its upper surface is much larger. In medial view, the labial process curves labially and basally well beyond the rest of the crown. The pulp cavity in the basal surface of the crown is very small, and extends only into the proximal part of the labial process.

The most highly specialized teeth (Text-fig. 23C) have the crown shallower, the occlusal margin flatter and more gently rounded, and the crest and paired depressions on the lingual surface more strongly marked. In these forms the depressions on the lingual face are in the form of rounded sockets. The labial process is enormously enlarged, so that the breadth of the tooth is greater than its length (ratio of breadth to length as low as 0·75). The process projects labially in a long, tongue-like flange. The pulp cavity in the basal surface of the crown is very small, and hardly extends into the base of the labial process.

In none of the teeth of this species is any trace of a root preserved. The basal surface of the crown and the wall of the small pulp cavity are always quite smooth and without the foramina usually present in teeth where the root has been broken or abraded off. In the more specialized teeth the pulp cavity and basal surface of the crown are both so small that if a root were present its value as an anchor would be negligible. The form of the teeth and of the basal surface and pulp cavity suggest that there may have been no root in this species, especially in the shallower, more

specialized teeth. This conclusion is supported by the inferred mode of articulation of the teeth (see below), which seems to allow no room for a root.

The Arrangement of the Teeth

As shown in Text-fig. 23, there is a great deal of variation in the teeth of *L. rhizion*, involving the depth of the tooth, the length of the labial process, and the symmetry of the tooth. I can find no correlation between these characters, except that the

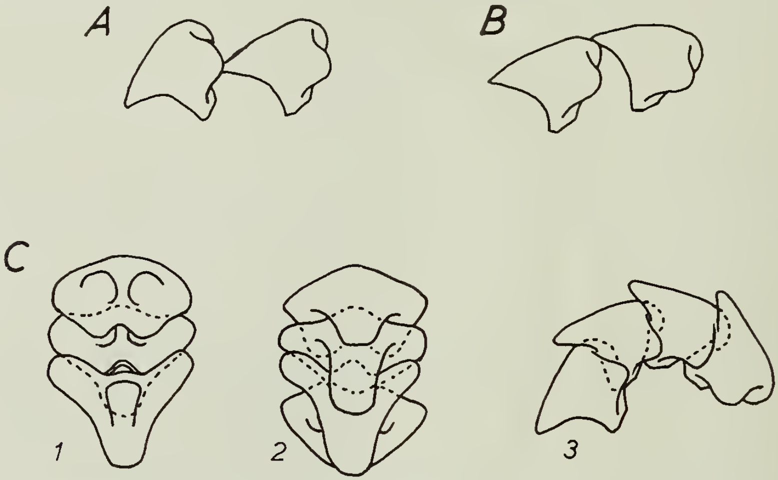


Fig. 24. *Lonchidion rhizion* sp. nov. Diagram showing possible modes of arrangement of the teeth, $\times 15$ approx. For explanation see text. Based on the holotype (Text-fig. 23*b*). A, B, C_3 in medial view ; C_1 in basal view ; C_2 in occlusal view.

labial process is normally longer in shallower teeth, but deep, asymmetrical teeth with rather long labial processes do occur. As yet, there is therefore no means of assigning the different teeth to a position in the mouth, but it is clear that the dentition of *L. rhizion* must have been strongly heterodont.

In none of the teeth of *L. rhizion* is there any well marked wear facet on the occlusal surface of the tooth. In *L. breve* there is often a vertical pressure scar in the centre of the lingual surface of the crown, caused by the tip of the labial process of the succeeding tooth : in *L. rhizion* there is never such a scar, but instead there is a central crest and a pair of depressions. These depressions are very weak in the deepest teeth with the largest pulp cavity (Text-fig. 23A), but become stronger as the depth of the tooth and the size of the pulp cavity decrease, until in the shallowest teeth (Text-fig. 23C) they are deep sockets. The apparent correlation (Text-fig. 23) between length of the labial process and strength of the lingual depressions does not hold good for all specimens. The shape and position of these lingual depressions and the crest between them suggest that they served for articulation between the teeth, and this is supported by the fact that they are strongest in teeth in which the pulp cavity (and basal surface of attachment) is smallest.

There are three possible ways in which the successive teeth in *L. rhizion* might have been arranged.

1. As in *L. breve* (Text-fig. 20), the teeth might have been arranged in a simple file, but without contact between successive teeth (since there is never a pressure scar on the lingual face which might be caused by the tip of the labial process of the succeeding tooth). This scheme is shown in Text-fig. 24A. It is very unlikely that the teeth were arranged in this way because it allows no function for the paired depressions and central crest on the lingual face of the crown of the shallower teeth ; because the enlargement of the labial process in the shallower teeth would also be without apparent function, and because the teeth with very long, slender labial processes (Text-fig. 23C) would give an unsatisfactory dental series.

2. The teeth might have been arranged as in Text-fig. 24B, with the labial surfaces forming the occlusal surface and the tip of the labial process of each tooth ending at the central cusp of its predecessor. Although this scheme gives a satisfactorily smooth occlusal surface to the dental series, it is open to the same objections as the scheme outlined above. The only function for the paired depressions on the lingual surface of the crown in this scheme would be to receive a pair of processes from the root of the succeeding tooth : this is unlikely, for if the roots were large enough to abut against the preceding tooth it is probable that they would be preserved in some specimens.

3. The teeth might have been arranged as in Text-fig. 24C, with the labial process of each tooth overlapping the central cusp of its predecessor. Manipulation of plasticine models of the teeth shows that in this type of arrangement the boss at top of the crest in the centre of the lingual surface would have fitted in the labial part of the pulp cavity of the succeeding tooth, and that the paired depressions would have articulated with the ridge or knob on each side of the pulp cavity at the base of the labial process. In this arrangement the radius of the tooth whorl would have been rather small, since a satisfactory fit between successive teeth is only obtained if their axes differ by about forty degrees. This scheme gives a function to the crest and paired depressions on the lingual face of the crown, gives a functional explanation of the elongation of the labial process, and gives each tooth series a radula-like occlusal surface which should be highly efficient. It does not give an entirely satisfactory fit between either the deep teeth with a short labial process (Text-fig. 23A) or the shallow teeth with a very long labial process (Text-fig. 23C), but with most of the specimens it is satisfactory. If the teeth were arranged in this way, part of the pulp cavity was occupied by the lingual crest of the preceding tooth and not by a root. In the shallowest teeth with the longest labial process the pulp cavity is so small that the articulation between the teeth would have left only a narrow channel lingually, through which nerves and vessels could have passed into the pulp cavity.

It is suggested, pending the discovery of more complete material, that *Lonchidion rhizion* was a shark in which a flattened but serrated grinding dentition was evolved by the labial process of each tooth overlapping the crown of its predecessor ; that this overlapping entailed drastic reduction and eventual loss of the root, and that this

was compensated for by the development of complex interlocking articulations between successive teeth.

Affinities. *Lonchidion rhizion* is known only from the Ashdown Beds (Cliff End bone-bed), where it is not common, and from the Wadhurst Clay (Telham bone-bed) and Grinstead Clay (Paddockhurst bone-bed), where it is rare. The least specialized teeth are very like the (presumed) anterior teeth of *L. breve breve*, and it is probable that the species evolved from *L. breve*, primarily by flattening and broadening of the labial process. *L. rhizion* is the only known shark in which some, at least, of the teeth were without roots.

Lonchidion heterodon sp. nov.

(Text-fig. 25)

Diagnosis. *Lonchidion* known only by isolated teeth, less than 4·0 mm. in length ; tricuspid symphysial teeth probably present, dentition heterodont ; crowns of teeth moderately elongated, ratio of breadth to length 2·5–4·5 (except in the presumed symphysial teeth, where the ratio is less than 2·0), crown shallower than broad in lateral teeth, deeper than broad in anterior and posterior teeth ; teeth *Hybodus*-like, with low central cusp and three pairs of lateral cusps (one pair in symphysial teeth), with striae diverging from occlusal crest, striae few and weak in anterior and posterior teeth, numerous and strong in large lateral teeth ; labial process strong in anterior and posterior teeth, weak in lateral teeth.

Holotype. P.47188 (Text-fig. 25A), a lateral tooth without root from the Upper Purbeck, Friar Waddon, Dorset.

Material. Twelve teeth, all without roots.

Horizons and localities. Upper Purbeck : Friar Waddon, Dorset (6 teeth). Ashdown Beds : Cliff End bone-bed, Cliff End, Sussex (5 teeth). Wadhurst Clay : Hastings, Sussex (1 tooth).

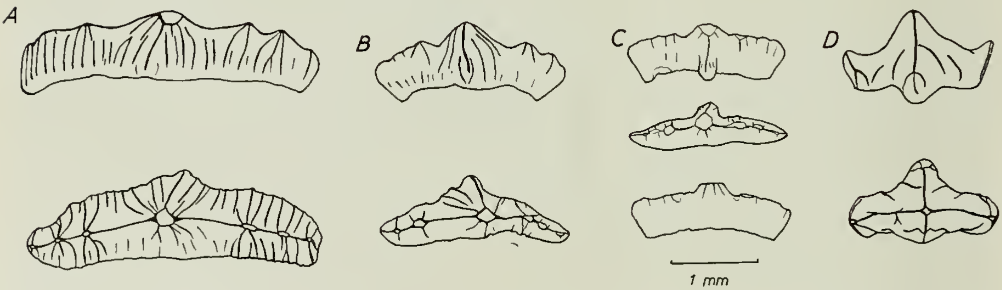


Fig. 25. *Lonchidion heterodon* sp. nov. Teeth in labial (above) and occlusal view, c also in lingual view (below). a. P.47188, lateral tooth, the holotype. b. P.47189, antero-lateral tooth. c. P.47192, posterior tooth. d. P. 47197, symphysial tooth tentatively referred to this species. a, b, c from the Upper Purbeck ; Friar Waddon, Dorset ; d from the Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex.

DESCRIPTION. The holotype is a broad, low-crowned tooth which is *Hybodus*-like in appearance, with a low central cusp and three pairs of lateral cusps. The occlusal crest is well marked. Both labial and lingual faces of the crown bear strong striae which reach the occlusal crest at the central and lateral cusps but fail to do so between the cusps. The striae are occasionally bifurcated basally, and are stronger and longer on the labial face than on the lingual. The labial process, below the central cusp, is poorly marked. Both the basal surface of the crown and the lingual surface are concave, and the tooth is strongly asymmetrical. The material contains seven teeth of this type, ranging in length from 2·5 to 4·0 mm., and in the ratio of breadth to length from 3·0–4·5. The asymmetry and curvature of the basal surface and occlusal crest are particularly characteristic of these teeth. Smaller teeth of this type grade into the type shown in Text-fig. 25B. which are about 2 mm. in length and have the crown higher and narrower. In these teeth the central cusp is stronger and the lateral cusps weaker than in the larger teeth, while the labial process is larger and the striae fewer and shorter. These teeth are still weakly asymmetrical, and have the basal surface and the labial surface concave. In the small tooth shown in Text-fig. 25C these trends go further : the crown is higher and narrower, the central cusp and labial process are accentuated, the lateral cusps and striae reduced. There is little difference between this tooth and examples of *Lonchidion breve crenulatum* (Text-fig. 17) from the Grinstead Clay.

Tentatively included in this species is the tooth shown in Text-fig. 25D. This is bilaterally symmetrical and must be a symphysial tooth. There is a large central cusp, a single pair of sharp lateral cusps, a large labial process, and a few coarse striae. In this tooth (length 1·7 mm.) the breadth and depth are almost equal, and the ratio of breadth to length is about 1·7, much less than in the other teeth of the species.

The material of this species, though very limited, suggests that the dentition was strongly heterodont and consisted of small, high-crowned symphysial teeth (Text-fig. 25D), large, broad, low-crowned lateral teeth (Text-fig. 25A), smaller, narrower antero-lateral and postero-lateral teeth (Text-fig. 25B), and posterior teeth which are very like *Lonchidion breve crenulatum* (Text-fig. 25C).

The root is not preserved in any specimen. In histological structure (seen in peels taken from ground, etched surfaces of a fragment of a lateral tooth from the Upper Purbeck) the crown of this species agrees exactly with *Lonchidion* : the crown is made up entirely of pallial dentine, the long, branched dentine tubules radiating from vascular canals at the base of the crown.

AFFINITIES. This species, though poorly known, is of interest and importance as the only record of *Lonchidion* in the Jurassic. The smallest teeth of the species, presumably posterior, are almost identical with those of *L. breve crenulatum* from the Grinstead Clay, but are linked by a series of intermediate forms with teeth like the holotype (Text-fig. 25A) which are very *Hybodus*-like (cf. *H. parvidens*—Text-fig. 7B ; *H. brevicostatus*—Text-fig. 13B) though still retaining the very thick pallial dentine which is typical of *Lonchidion*. *L. heterodon* is rare at Cliff End, in the Ashdown Beds ; and is known above this only by a single lateral tooth from the Wadhurst

Clay. If we assume that *L. heterodon*, as the earliest known species of *Lonchidion* shows the most primitive condition, the genus must have originated as a heterodont, low-crowned, *Hybodus*-like form with very thick pallial dentine. The more homodont species, *L. breve*, would then have evolved by adoption in all the teeth of the slender, high-crowned, almost smooth form of the posterior teeth in *L. heterodon*, and by increasing the overlap between adjacent files of teeth.

Fin Spines and Cephalic Spines of Lonchidion

In the late Cretaceous species *Lonchidion selachos*, Estes (1964 : 9) was able to include fragmentary fin spines and cephalic spines from localities at which teeth of the species occur. There is little doubt of the association between the teeth and the spines since *L. selachos* is the only hybodont known from the deposits. In the British Wealden and Purbeck the matter is complicated by the presence of small and immature hybodonts of other species.

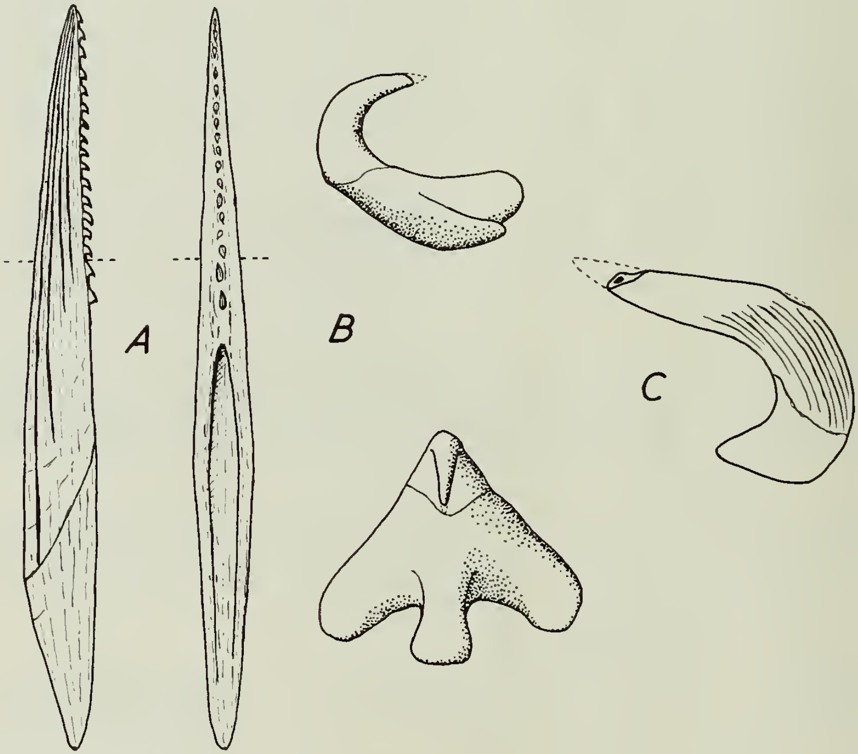


FIG. 26. *Lonchidion* sp. A. Dorsal fin spine, a restoration based mainly on P.29995, Wealden ; Isle of Wight, P.12815, Weald Clay ; Bookhurst, Surrey, and P.47208, Weald Clay ; Henfield, Sussex, in lateral (left) and posterior view, $\times 1\frac{1}{2}$ approx. The broken line marks the plane of the section shown in Pl. 3, fig. 4. B. Cephalic spine, P.11895 from the Wadhurst Clay ; Brede, Hastings, Sussex, in dorsal (below) and lateral view, $\times 3{\cdot}5$ approx. C. Incomplete cephalic spine in lateral view, P.47207, Weald Clay ; Henfield, Sussex. $\times 6{\cdot}5$.

In *L. selachos* the cephalic spine (Text-fig. 27E) has a weakly lobed root, no barb at the tip, and is ornamented with small tubercles which are drawn out into ridges distally and are pointed anteriorly. The spine is about 10 mm. in length, roughly 2·5 times as long as the average lateral tooth of the species. Among the material from the Cliff End bone-bed there are several worn and incomplete cephalic spines of small size : a complete spine of this type from the Wadhurst Clay was figured by Smith Woodward (1916, pl. 1, fig. 4). These spines (Text-fig. 26B) differ from the cephalic spine assigned to *L. selachos* in that the root is much wider and more sharply divided into three lobes, and the enamelled exserted part of the spine lies at a much shallower angle to the root and does not curve back so far. In all the specimens from Cliff End the enamelled part of the spine is perfectly smooth, but this could well be due to abrasion, for in a similar spine (P.12813) from the Weald Clay of Bookhurst, Cranley, Surrey, there are vertical striae at the base (the only part preserved) of the exserted portion. These cephalic spines are tentatively referred to *Lonchidion* : probably they belong to *L. breve*, the commonest species at Cliff End.

A single cephalic spine from the Weald Clay of Henfield (P.47207, Text-fig. 26C) is also probably a *Lonchidion*. The root is almost entirely missing but the crown curves back in just the same way as in *L. selachos*, much more strongly than in the Cliff End and Wadhurst Clay spines. The tip of the spine is smooth and without a barb, but the proximal part of the crown is ornamented with about twelve sub-parallel striae, quite a different form of ornamentation from *L. selachos*. This cephalic spine is perhaps from *L. striatum*, the dominant species of *Lonchidion* at Henfield.

The fin spines of *L. selachos* (Text-fig. 27F) are all incomplete, so that the total length cannot be measured, but they reached at least 5 mm. in breadth, and were probably about 5 cm. long. The surface is apparently without enamel ridges and is marked only by the weak striations of the texture of the superficial osteodentine. There is a single series of denticles on the posterior face.

There are no complete fin spines among the bone-bed material described here, and the fragments of spines from Cliff End and Paddockhurst are too worn for description. But fragmentary spines from the Weald Clay of Henfield and Bookhurst, Cranley, Surrey, and from an unknown horizon (? *Perna* Bed) in the Isle of Wight seem to be referable to *Lonchidion*, although it is only in the few examples where part of the inserted base is preserved that one can distinguish with certainty between small spines and the tips of large spines of *Hybodus*. From these fragments one can reconstruct the fin spine of Wealden *Lonchidion* (Text-fig. 26A). The spines reached about 7 cm. in length and were almost straight, the posterior border of the spine showing a slight curvature in its distal part. The exserted part of the spine is ornamented with enamel ridges. One ridge forms a keel on the anterior border of the spine. On the proximal part of the spine there are two or three ridges near the anterior border, the posterior part of the lateral surface being smooth. Towards the tip, the number of ridges increases to about five, equally spaced on the lateral surface. The ridges are straight and do not anastomose or bifurcate. The denticles on the posterior face of the spine are in a single series, although towards the base they may be placed alternately to the right and left of the mid-line, indicating their origin from paired series.

I have seen no examples of the double or rudimentary paired denticles of the type described in *H. brevicostatus* (p. 308). The denticles are smooth and without striae: at the tip of the spine they are low and long based, proximally the bases are shorter and the denticles higher and recurved. In no specimen is a complete series of denticles preserved, but there cannot have been more than about twenty or twenty-five. In histological structure (Pl. 3, fig. 4) the spines consist of the usual outer layer of osteodentine with an inner layer of lamellar tissue in the exserted part of the spine. The lamellar tissue makes up from half to two-thirds of the wall of the spine at about the middle of its length.

These spines agree with those which Estes (1964 : 11) assigns to the late Cretaceous *L. selachos*, particularly in the lack of curvature and the form and position of the posterior denticles, but they differ in retaining a few enamel ridges on the lateral surfaces.

The Affinities of **Lonchidion**

The only other species of *Lonchidion* known is *L. selachos* Estes (1964) from fresh-water deposits of late Cretaceous age in Wyoming, where isolated teeth are fairly common at a number of localities. The lateral teeth of *L. selachos* (Text-fig. 27A) are very like those of *L. breve breve* in the smooth crown, large hybodontoid root,

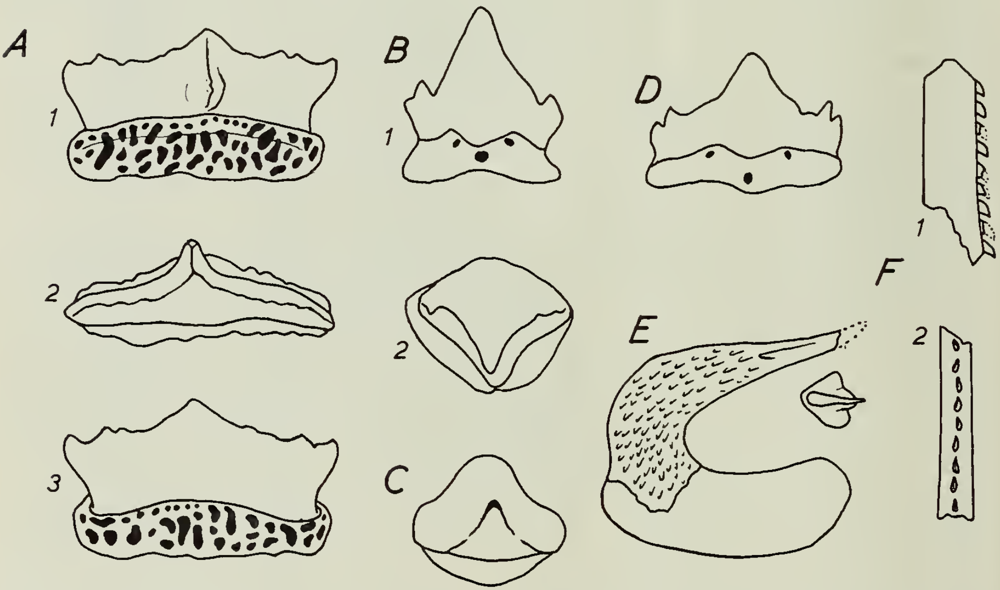


Fig. 27. *Lonchidion selachos* Estes. A. Lateral tooth (the holotype) in labial (1), occlusal (2) and lingual (3) view, ×9. B. Symphysial tooth in lingual (1) and occlusal (2) view, ×11. C. Symphysial tooth in basal view, ×11. D. Parasymphysial tooth in lingual view, ×11. E. Cephalic spine, the base restored, in lateral view, ×3·5, and (inset) in dorsal view, ×$\frac{2}{3}$. F. Fragment of dorsal fin spine in lateral (1) and posterior (2) view, ×2. All from the Lance Formation; Wyoming, U.S.A. After Estes (1964).

waisted root/crown junction, labial process, and histological structure, but they have the occlusal crest produced into fairly well marked cusps : teeth of *L. breve breve* tending towards this type occur high in the Wealden (see p. 316). In size they range from 2–6 mm., a little larger than *L. breve*. Estes suggests that this type of tooth occupied only the lateral and posterior parts of the mouth, and that the anterior teeth were of the type shown in Text-fig. 27B, C, D, high-crowned teeth with one or two pairs of lateral cusps, no labial process, and squatinoid roots (Casier 1947*a* : 10) with a central canal. In the British Wealden and Purbeck, although several hundred teeth of *Lonchidion* have been examined, no teeth of this type have been found. Although it is possible that in *Lonchidion* the anterior teeth could, by the Upper Cretaceous, have evolved a squatinoid root, in parallel with the heterodontids, it seems equally probable that the teeth described by Estes belong to a squatinid or orectolobid, perhaps to his species *Squatirhina americana* or a related form.

Estes compares the lateral teeth of *L. selachos* with teeth from the German Keuper described as *Palaeobates spinosus* by Seilacher (1943, text-figs. 27, 28). The lateral teeth of *P. spinosus* are typical of the genus, flattened *Heterodontus*-like teeth which bear little resemblance to *Lonchidion* except in their histological structure. But Seilacher assigns to the posterior part of the jaws of *P. spinosus* very small teeth (less than 1 mm. in length) which are very like those of *Lonchidion*, with a strong labial process, a waisted root/crown junction and a smooth crown. As Estes notes, no teeth of this type occurred in Stensiö's (1921 : 35) material of associated *Palaeobates* teeth from the Trias of Spitsbergen, and the systematic position of these small teeth is by no means certain. Teeth of this type are clearly fairly abundant in the German Trias : acid treatment of a small block of bone-bed from the Muschelkalk of Crailsheim (28466) has yielded several isolated crowns which are almost indistinguishable from *Lonchidion breve breve*. Until more complete information on these Triassic forms is available it is impossible to decide whether they are related to *Lonchidion* or are convergent, particularly since no Lower Jurassic teeth resembling *Lonchidion* are known. Estes also draws attention to the resemblance between the teeth of *Lonchidion* and those of the only other freshwater hybodont, the Triassic *Lissodus africanus* (Broom) (Brough 1935, pl. 2).

Glikman (1964) has recently proposed a radical reclassification of selachians. He divides the sharks and rays among two infraclasses, Orthodonta and Osteodonta, mainly on the basis of the histological structure of the teeth. In Orthondota the crown of the tooth consists of orthodentine, in Osteodonta of osteodentine surrounded by pallial dentine. Glikman finds these two groups to have been distinct since their first appearance in the Devonian. He places the hybodontids and ptychodonts in the Osteodonta, and makes a new family Polyacrodontidae, order Polyacrodontida and superorder Polyacrodonti within the Orthodonta for *Polyacrodus* and *Palaeobates*. Thus Glikman believes that *Polyacrodus* and *Palaeobates* on the one hand and the hybodonts on the other represent lines which have evolved independently since the Devonian and are only very distantly related. Because of the structure of the teeth, both *Lonchidion* and *Lissodus* would be placed in the Orthodonta, presumably in the Polyacrodonti, though the regular

alternation of the teeth in adjacent series which occurs in *Lissodus* and in some species of *Lonchidion* (see p. 319) is not a character of Polyacrodonti according to Glikman. Thus Glikman's major subdivision of the sharks makes it necessary to believe that *Lissodus* and *Lonchidion* are only related to the well known Jurassic and Lower Cretaceous species of *Hybodus* in so far as the Orthodonta and Osteodonta shared a hypothetical common ancestry in the Lower Devonian. Yet *Lissodus* and *Hybodus* share such characters as fin spines of exactly similar form and structure, the anterior spine lying more obliquely than the posterior (Brough 1935), a posteriorly placed anal fin, the presence above the eyes, in males only, of two pairs of cephalic spines of similar form, etc. That such features as these should have been acquired independently and roughly simultaneously in two unrelated groups seems extremely unlikely. Another selachian group in which teeth composed either of osteodentine or orthodentine occur in closely related forms is the Upper Cretaceous sub-family Ganopristinae of the pristid sawfishes (Schaeffer 1963). In the ganopristines the rostral teeth of forms like *Onchopristis*, *Sclerorhynchus* and *Ganopristis* have a crown of orthodentine, while *Onchosaurus* and *Pucapristis* (like the Tertiary and living Pristinae) have a crown of osteodentine. Close relationship between these various genera seems beyond doubt. I am therefore unable to accept Glikman's Orthodonta and Osteodonta, at least so far as the Mesozoic sharks are concerned. I believe that the thickness of the pallial dentine and the presence or absence of osteodentine are features which have changed a good deal in the history of the sharks, that these characters cannot be used to define major subdivisions, and that there are as yet no satisfactory grounds on which forms such as *Polyacrodus*, *Palaeobates*, *Lissodus* and *Lonchidion* can be separated from the Hybodontidae. At present, all that can be said of the origins of *Lonchidion* is that the fin spines and cephalic spines ally it with the Hybodontidae, the histological structure of the teeth is like *Polyacrodus*, and that the teeth in the earliest known species, *L. heterodon*, are more like those of *Hybodus* than they are in later species. Similar forms (*Lissodus*) were already present in fresh water in the Trias.

Lonchidion is evidently a genus of hybodont which became adapted to life in fresh water in or before the Upper Jurassic, and underwent considerable radiation there, producing *Polyacrodus*-like forms (*L. striatum*) and highly specialized forms in which the roots of the teeth were lost (*L. rhizion*), both these being short-lived, while the more generalized types (*L. breve*, *L. selachos*) continued through almost to the end of the Cretaceous as the last survivors of the hybodonts. The relationships between the species of *Lonchidion* are summarized in Text-fig. 31.

Family **PTYCHODONTIDAE**

Amended diagnosis. Hybodont sharks in which there are no fin spines or cephalic spines ; vertebral centra possibly calcified ; jaws elongated, with teeth confined to their broad symphysial region ; teeth flattened and crushing, dentition heterodont ; nine or less paired files of teeth and an unpaired symphysial file in each jaw ; largest and most specialized teeth, which are rhombic or rectangular, at or

near the symphysis, teeth decreasing in size posteriorly; crowns of teeth with strong ridges or crests of enamel; crown made up mainly of osteodentine; roots of teeth hybodontoid.

Genus *HYLAEOBATIS* Smith Woodward 1916 : 19

Amended diagnosis. Ptychodont sharks known only by isolated teeth; jaws probably very broad, dentition probably similar in both jaws; a symphysial file and eight paired files of teeth in each jaw; symphysial teeth rectangular, three or four times as long as broad, parasymphysial teeth rectangular, about two-and-a-half times as long as broad; second paired lateral teeth rhomboid, remaining teeth more or less ovoid and *Acrodus*-like, not so closely apposed as anterior teeth; crowns of teeth with occlusal crest near labial margin in anterior teeth, central in posterior teeth; fine bifurcating and anastomosing striae radiating from occlusal crest; histological structure of crown like that in *Acrodus*, vascular canals less regularly arranged than in *Ptychodus*.

Type species. *Hylaeobatis ornata* (Smith Woodward), the only species.

Hylaeobatis ornata (Smith Woodward)

(Pl. 4; Pl. 5, figs. 4–7; Text-figs. 28–30)

1889 *Acrodus ornatus* Smith Woodward : 296, pl. 13, fig. 10.
1916 *Acrodus ornatus* Smith Woodward; Smith Woodward : 14, pl. 2, figs. 15–18.
1916 *Hylaeobatis problematica* Smith Woodward : 19, pl. 5, figs. 1–5, text-fig. 10.

Diagnosis. As for genus; symphysial teeth reaching about 15 mm. in length.

Holotype. P.5275, posterior tooth without root, probably from the Wealden Shales, Brixton, Isle of Wight.

Material. In addition to the holotype, about 300 teeth, all but ten without roots.

Horizons and localities. Weald Clay: Henfield, Sussex; Crowhurst, Surrey; Bexhill, Sussex; Meadvale, Redhill, Surrey; Hastings, Sussex; Sevenoaks, Kent. Wealden Shales: Brook, Brixton, Yaverland and Atherfield Point, Isle of Wight. Lower Greensand: *Perna* Bed, Sandown, Isle of Wight; Sandgate Beds, Godalming, Surrey (derived).

Description. The new material of this species from Henfield, consisting of almost three hundred teeth (mostly without roots), allows one to attempt a restoration of the dentition and shows that the two species *Acrodus ornatus* and *Hylaeobatis problematica* are synonymous, the first having been established for the small posterior teeth and the second for the large anterior teeth.

The material from Henfield includes nine complete teeth in which the roots are preserved: the dimensions of these teeth are shown in Table II. Among these nine complete teeth, seven distinct types are present, the two pairs P.47212, P.47218 and P.47213, P.47217 being of the same type. Two more types of tooth are represented among the incomplete teeth.

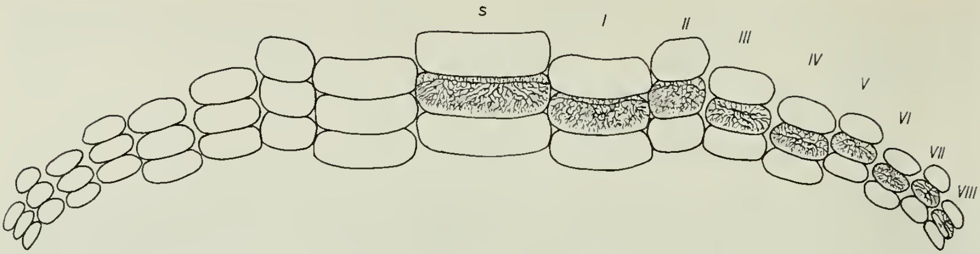


FIG. 28. *Hylaeobatis ornata* (Smith Woodward). Restoration of the dentition of one jaw in occlusal view, × 1·5 approx. ' s ', symphysial file ; I–VIII, paired files. The surface pattern of one tooth in the symphysial file and each of the right hand files is drawn from examples from the Weald Clay of Henfield, Sussex.

1. Symphysial teeth. The largest and broadest of the complete teeth, P.47211, (Pl. 4, fig. 1 ; Text-fig. 28 ' S ') is perfectly bilaterally symmetrical and has a clearly marked ridge in the centre of the basal surface of the root : this must be a symphysial tooth, and the ridge marks the symphysis between the two rami of the jaw. In shape the tooth agrees with a worn specimen figured by Smith Woodward (1916, pl. 5, fig. 3), and among the teeth from Henfield there are nine rootless examples of this type, ranging in length from 7–15 mm., and in the ratio of breadth to length from 2·8–3·5. The labial face of the crown is strongly convex in the vertical plane, weakly concave in the horizontal. The lingual face is strongly concave vertically and weakly convex horizontally. The lateral ends of the crown are rounded in P.47211, but in other specimens they may show two pressure scars, giving a hexagonal coronal surface. In P.47211 the crown is quite unworn. The coronal surface is divided into a narrow labial zone and a broad lingual zone by a clearly marked longitudinal ridge. Comparison with the less specialized posterior teeth shows that this ridge is the occlusal crest. The labial zone, which makes up about a quarter of the surface of the crown, slopes sharply downwards, and is ornamented with bifurcating ridges which pass out from the occlusal crest to end about half way between this crest and the root/crown junction. The lower half of this sloping labial surface of the crown fitted in life in the hollow on the lingual face of the crown of the preceding tooth. The broad lingual zone of the crown is almost flat, and formed the occlusal surface of the tooth. It is ornamented with striae which originate at the occlusal crest and which bifurcate and anastomose frequently as they pass lingually, so that the lingual half of the crown has a reticular surface. The strongly concave lingual face of the crown is separated from the coronal surface by a sharp angle, and is smooth except for coarse irregularities near the root/crown junction.

2. Parasymphysial teeth. P.47212 (Pl. 4, fig. 2 ; Text-fig. 28, I) is a tooth in which the crown is elongated, broad and flat, as in the symphysial teeth, but is clearly asymmetrical and is shorter and proportionally broader than in the symphysial teeth. As one would expect, teeth of this type are about twice as common as the symphysial teeth : there are about twenty incomplete examples among the material from Henfield. The tooth figured by Smith Woodward (1916) in Pl. 5, fig. 4, is a worn

TABLE II

The dimensions (in mm.) of nine complete teeth of *Hylaeobatis ornata* from the Weald Clay of Henfield, Sussex

Specimen	Length of crown	Length of root	Total depth	Depth of crown	Depth of root	Breadth of crown	Breadth of root	Length of crown / Breadth of crown	Length of crown / Total depth	File to which assigned
P.47211	14·0	12·7	6·9	2·8	3·6	4·0	3·2	3·5	2·2	S
P.47212	10·6	9·3	5·5	2·7	2·3	4·1	3·0	2·6	2·0	I
P.47218	9·4	8·0	5·0	2·5	2·2	4·2	2·6	2·2	1·9	I
P.47213	5·8	5·3	5·3	3·0	2·1	4·2	3·0	1·4	1·1	II
P.47217	3·9	3·1	4·0	1·7	2·0	2·7	1·8	1·4	1·0	II
P.47214	6·7	6·1	3·9	2·0	1·7	3·3	2·2	2·0	1·7	IV
P.47219	5·3	4·9	2·4	1·0	1·0	1·8	1·2	2·9	2·2	V
P.47215	4·7	4·9	2·8	1·3	1·2	2·3	1·6	2·0	1·7	VI
P.47216	3·0	3·2	2·0	1·0	0·7	1·1	0·9	2·7	1·5	VIII

example of this type. These teeth range from 6–12 mm. in length, and in the ratio of breadth to length from 2·6 to 3·0. The crown is shaped like that of the symphysial teeth, being weakly concave labially and convex lingually in the horizontal plane, with the occlusal crest near the labial margin, a steeply sloping labial zone, and similar ridged and reticulate ornament. The crown is deeper at one end than at the other, and the deeper end of the crown commonly bears a pair of pressure scars caused by contact with the teeth in the adjacent file. The lower end of the crown is often without pressure scars, as in the specimen figured by Smith Woodward. These teeth are almost certainly parasymphysial teeth from the first paired files in the jaws, the deeper end of the crown being medial and the pressure scars at this end being caused by contact with the large symphysial teeth.

3. Antero-lateral teeth. P.47213 (Pl. 4, fig. 3 ; Text-fig. 28, II) is an example of a third and very distinctive type of tooth, in which the crown is short and very broad, with a ratio of breadth to length often less than 1·5, and the total depth almost equal to the length of the crown. The crown of this type of tooth is strongly asymmetrical. The material from Henfield contains about twenty-five teeth of this type, ranging in length from 4–8 mm. and in the ratio of breadth to length from 1·3–1·8. The holotype of *H. problematica* (Smith Woodward, 1916, pl. 5, fig. 1) and two more of Smith Woodward's figured specimens of this species (1916, pl. 5, figs. 2, 4) are of this type. In these teeth the ornamentation of the crown is very like that in the symphysial and parasymphysial teeth, but the occlusal crest does not lie so near to the labial margin of the crown, and there is often an area of reticulate ornamentation lying labial to this ridge, a feature which is not seen in symphysial and parasymphysial teeth. As in the parasymphysial teeth, one end of the crown is deeper than the other : this deeper end is commonly marked by pressure scars whereas the shallow end is almost always without pressure scars. The concavity on the lingual face of the crown, in which the labial margin of the succeeding tooth fitted, is much stronger at the deeper end of the crown than at the shallower. These facts show that the deeper end of the crown is medial, that these teeth were in close contact medially with their neighbours in both the same and the adjacent file, but that laterally these contacts, particularly with teeth in the adjacent file, were less close. The teeth are probably members of the second paired files in the jaws, next to the parasymphysials, the two types of teeth being equally common. These antero-lateral teeth show the strongest asymmetry of all the teeth.

4. Lateral and posterior teeth. The three types of teeth described so far, the symphysial, parasymphysial and antero-lateral, all have the crown approximately rectangular or rhomboid in shape, with a broad, flat coronal surface and with the occlusal crest near the labial margin. The remainder of the teeth from Henfield do not show these features : the crown is ovoid in shape, its surface is more or less rounded, and the occlusal crest lies at or near the centre of the crown. The distinction between these two classes of teeth is not absolute, intermediates between the two being found in some of the antero-lateral teeth, where the crown may be moderately rounded and have the occlusal crest some distance from the labial margin, and in some of the larger lateral teeth. These intermediate forms and the relative

abundance of the different types of teeth leave little doubt that the two classes of teeth are correctly placed in the same species. The symphysial, parasymphysial and antero-lateral teeth, interpreted as representing five files (one median and two paired) make up a little less than one-third of the sample from Henfield (68 out of 215 teeth) : this proportion gives some support to the conclusion, reached on morphological grounds, that there was a total of seventeen files of teeth in each jaw.

P.47214 (Pl. 4, fig. 4 ; Text-fig. 28, IV) is an example of one of the larger lateral teeth. The crown is approximately ovoid in outline. The occlusal crest of the crown, though not strongly marked in this specimen, lies nearer to the centre of the crown than to the labial margin. The ornamentation of the crown consists of bifurcating and anastomosing striae, diverging from the occlusal crest and forming a reticulum towards the margins of the crown, including a reticular area towards the labial margin, as in the antero-lateral teeth. The material from Henfield contains about fifty teeth agreeing with this specimen, ranging in length from 4·0–7·5 mm. and in the ratio of breadth to length from 1·9–2·7. Like the parasymphysial and antero-lateral teeth, these specimens are asymmetrical, with the medial end of the crown a little higher than the lateral. Pressure scars on the ends of the teeth are rare, and these teeth were evidently not closely associated with the neighbouring files. These teeth are interpreted as forming the third and fourth paired files of teeth in each jaw.

Among the remaining teeth from Henfield, two more distinct types can be easily recognized, a long, narrow type, and a short, broad type, both including only small teeth. The long, narrow teeth (P.47216, Pl. 5, fig. 6 ; Text-fig. 28, VIII) range in length from 3·0–5·0 mm., with a ratio of breadth to length between 2·7 and 3·2. The crown is an elongate ovoid in shape. In the larger examples the ornamentation of the crown is irregular, though an occlusal crest in the centre of the crown can normally be recognized, from which bifurcating and anastomosing ridges diverge, forming a reticular pattern towards both lingual and labial margins of the crown. The occlusal crest curves lingually at each end of the crown. In smaller teeth of this type the ornamentation is more regular, with a strongly marked occlusal crest which curves lingually at the ends of the crown and forms a weak central cusp in the centre. The lingual half of the coronal surface is almost smooth in the smallest teeth, but usually bears a ridge, running parallel to the occlusal crest, which is joined to the central cusp and curves lingually without reaching the ends of the crown. The labial half of the crown bears two or three similar longitudinal ridges, joined to the central cusp and turning labially before reaching the ends of the crown. The holotype of *Acrodus ornatus* Smith Woodward (P.5275 ; 1889, pl. 13, fig. 10) is a worn tooth of this type, and among the material from Henfield there are about twenty-five examples.

The short, broad teeth (Text-fig. 28, VII) in none of which is the root preserved, agree with the long narrow teeth described above in all features of ornamentation, but are typically 3–4 mm. in length and 1·6–2·1 mm. in breadth, with a ratio of breadth to length of 1·6–1·9. They show the same increasing regularity of ornamentation with decreasing size, with the appearance in small forms of ridges running parallel to the occlusal crest. The crown in these teeth is almost semicircular in

shape, with a flat lingual margin and a strongly arched labial one. A tooth of this type is figured as *Acrodus ornatus* by Smith Woodward (1916, pl. 2, fig. 18), and there are about thirty examples among the material from Henfield.

There remain undescribed about fifty teeth from Henfield, which are intermediate in shape and ornament between the large lateral teeth (III, IV) and the small teeth of short, broad (VII) and long, narrow (VIII) type. In these teeth (P.47215; Pl. 5, fig. 7) the crown is ovoid in shape, 3·0–7·0 mm. in length, and with a ratio of breadth to length of 1·9–3·0. The larger of these, 4·5–7·0 mm. in length, are narrower, with the ratio of breadth to length usually between 2·5 and 3·0, while the smaller teeth, 3·0–4·5 mm. in length, are broader, with the ratio of breadth to length from 2·0 to 2·5. The labial margin of the crown is usually more strongly curved than the lingual. An occlusal crest is normally recognizable in the centre of the crown, with bifurcating and anastomosing striae diverging to form a reticular pattern at both lingual and labial margins. One specimen figured as *Acrodus ornatus* by Smith Woodward (1916, pl. 2, fig. 17) is a worn tooth of this type. Of each of the paired types of teeth described above, the material from Henfield normally contains between twenty and thirty examples. This material contains about fifty of these ovoid teeth, and they probably represent two paired files in the postero-lateral part of the jaw (Text-fig. 28, V–VI).

5. The Root. There is no significant variation in the shape or structure of the root between the small posterior teeth and the large symphysial teeth. In all the teeth the root is typically hybodontoid (Casier 1947*a* : 9) in structure : porous and trabecular, with an irregular series of large foramina in both the lingual and labial surfaces (Pl. 4). The labial face of the root is concave, and is clearly marked off from the flat basal surface, which slopes lingually. The lingual face of the root is strongly convex, its upper part sloping out in a ledge which is largest in the anterior teeth, where it fitted against the concavity on the labial face of the root of the succeeding tooth. The root is shorter and narrower than the crown in all but the smallest posterior teeth (Pl. 5, figs. 6, 7). In the posterior teeth the root is shallower than the crown, but in the large anterior teeth it may be as deep as or deeper than the crown.

6. Histological Structure. Smith Woodward (1916 : 20, text-fig. 10) has given a brief account of the histological structure of the crown, which he compares with that of *Ptychodus*. Sections of the crowns of a large anterior tooth and a small posterior one are shown in Pl. 5, figs. 4, 5. The structure of the crown seems to be closer to that of *Acrodus* (Owen 1840, pl. 14), with which it agrees in the rather sparse and irregularly arranged vascular canals and the ' bunching ' of the tubules of the thin pallial dentine where they arise from the vascular canals. In *Ptychodus* the vascular canals are more regularly and closely arranged, and are parallel throughout the distal part of their length, as they are in the teeth of rays (Casier 1953, pls. 1, 2).

7. Other remains. There are no shark vertebrae associated with the abundant teeth of *Hylaeobatis* at Henfield, suggesting that the notochord was uncalcified, as in the hybodontids, or that the centra were very weakly calcified. As all the fin spines from Henfield are of normal hybodont type and seem to belong either to *Hybodus basanus* or to *Lonchidion*, there is no evidence that fin spines were present in *Hylaeobatis*.

Restoration of the dentition. On the basis of the morphology and relative abundance of the various types of teeth described above, a tentative reconstruction of the jaw of *Hylaeobatis ornata* has been made (Text-fig. 28). This reconstruction is largely hypothetical in that there is, as yet, no means of distinguishing between teeth from the upper and lower jaws, and one cannot discover whether there was any difference between the arrangement of the teeth in the two jaws, as there was in *Ptychodus*. But since only one type of symphysial tooth has been found, which when worn has a single, centrally placed wear facet, any variation between the two jaws is unlikely to be of the type seen in *Ptychodus*, where the symphysial teeth are large in one jaw and small in the other (Smith Woodward 1888 : 296). Smith Woodward (1916 : 21, pl. 5, fig. 4) has described one antero-lateral tooth of *Hylaeobatis* as showing signs of having been opposed by two teeth in life, but this is not true of any of the teeth from Henfield, and at present there is no good evidence of dissimilarity between the two jaws.

Since the symphysial teeth are the largest teeth, with the flattest crowns, the most labially displaced occlusal crest, and the closest fit with their neighbours in the same and adjacent files, the very broad, weakly curved dentition suggested in Text-fig. 28 seems the most reasonable interpretation of the material. As the crowns of the symphysial and parasymphysial teeth are slightly concave forwards, the medial part of the dentition must have been transversely placed and without appreciable posterior curvature. The strongly asymmetrical antero-lateral teeth (II) must mark the transition between the transversely placed, pavement-like dentition of the front of the mouth and the more *Acrodus*-like teeth of the last six files, which were probably curved back towards the articular region of the jaws. The asymmetry of the antero-lateral teeth and the close fit with the parasymphysial teeth which is indicated by the pressure scars on their medial faces show that these teeth must have curved forwards, as shown in Text-fig. 28. Because of this, it is difficult to see how the curvature of the posterior part of the jaw could have been greater than that shown in the figure, if the files of teeth were in reasonably close contact. All this suggests that the jaws of *Hylaeobatis* were very broad anteriorly, and that the dentition was largely confined to the anterior, transverse part of the jaw, as more complete remains show that it was in *Ptychodus* (Smith Woodward 1904). The transition between the small, *Acrodus*-like posterior teeth and the large, flattened teeth at the symphysis shows how a ray-like dentition can be produced in a hybodont by specializations which include the shifting labially of the occlusal crest, so that the occlusal surface is formed by the lingual face of the crown, the hollowing out of the lingual face of the crown to give increased contact between successive teeth, and the development of a rough surface by anastomosis between the surface striae. The variability in the occurrence and size of the pressure scars on the lateral and medial surfaces of the crowns of the anterior teeth suggests that in *Hylaeobatis*, just as in *Ptychodus*, the teeth in adjacent files did not alternate regularly in position as they do in the rays.

The Affinities of **Hylaeobatis**

Smith Woodward (1916 : 19) placed *Hylaeobatis* in the Myliobatidae, but compared it with *Ptychodus* (which he then included in the same family) and suggested that it

might be intermediate between *Ptychodus* and the cestracionts (including hybodonts). Later (1932 : 83) he included the genus in the Ptychodontidae. Casier (1953) has discussed the origin and affinities of the ptychodonts in some detail, and has shown that they are almost certainly specialized derivatives of the hybodonts or heterodontids, probably the former. He considered (p. 34) *Hylaeobatis* to be as close to the heterodontids as to the ptychodonts, and saw in it ' une forme intermédiaire, au point de vue de la morphologie dentaire, entre les Hybodontiformes et les Ptychodontes '. More recently (1961 : 45, pl. 5, fig. 1), in describing as *Hylaeobatis?* sp. a tooth from the Neocomian of the Congo, Casier revised this opinion and concluded that *Hylaeobatis* is probably a pycnodont. The tooth described by Casier seems to bear little resemblance to *Hylaeobatis*, particularly in the ornamentation of the occlusal surface and the flat, ornamented lingual face, and is probably a pycnodont tooth.

The new material described here seems entirely to confirm Smith Woodward's and Casier's (1953) opinions on the affinities of *Hylaeobatis*. *Hylaeobatis* shows unmistakable signs of hybodont relationships in the *Acrodus*-like posterior teeth and histological structure of the crown, and in the hybodontoid roots of the teeth. On the other hand, there are equally important indications of relationship with *Ptychodus*. Casier (1953 : 25) considers that the ptychodont type of dentition evolved from hybodonts with undifferentiated dentition by specialization of the anterior teeth and reduction in the number of files of teeth (in contrast to the heterodontids, where the lateral teeth are specialized, the anterior teeth remaining small). *Hylaeobatis* exhibits the most important character of the ptychodonts, the enlargement and specialization of the anterior teeth, with the symphysials and parasymphysials the most specialized. As to the number of files of teeth, *Ptychodus decurrens*, which seems to be the least specialized of the well known species (see below), has only five or six paired files in addition to the symphysials, but in later species the number of paired files rises (perhaps secondarily) to eight in *P. mortoni* (Williston 1900 : 238) and to nine in the Upper Senonian *P. mediterraneus* (Canavari 1916 : 37). *Hylaeobatis*, with eight paired files and a symphysial, agrees with *P. mortoni* and with hybodontids such as *Acrodus curtus* (=*A. anningiae*) (Smith Woodward 1889, text-fig. 10). The number of paired files is rather variable in hybodontids (9 or 10 in *H. basanus*, 9 in *H. brevicostatus*, six in *Asteracanthus*), and too much importance should not be attached to it. In the apparent absence of fin spines *Hylaeobatis* agrees with *Ptychodus* and differs from the hybodontids, in the apparent absence of calcified centra it agrees with the hybodontids (the evidence for the presence of calcified centra in *Ptychodus* is not conclusive—see below).

There seems little doubt that *Hylaeobatis* is intermediate between the hybodontids and *Ptychodus*. The genus is placed in the Ptychodontidae because it already exhibits the specialization of the anterior teeth which is characteristic of this family. There are two further points to be considered : the origin of *Hylaeobatis* and the ptychodontids, and the nature of the relationship between *Hylaeobatis* and *Ptychodus*.

The Origin of **Hylaeobatis**

Casier argues that forms with a ptychodont dentition, with the anterior teeth the largest and most specialized, must have evolved from hybodontoids in which the

dentition was homodont, without the enlargement of the lateral teeth which is characteristic of most hybodontids and of heterodontids. Also, since the anterior teeth of *Hylaeobatis* are the most specialized, it seems reasonable to assume that the small posterior teeth will retain most resemblance to the ancestral form. In the Weald Clay at Henfield, where teeth of *Hylaeobatis* are very abundant, there is an almost perfect gradation between the smaller posterior teeth of this genus and teeth of *Lonchidion breve breve*, a hybodontid species in which the dentition was probably almost homodont (see p. 314). In the smallest teeth of *Hylaeobatis* (Text-fig. 29C), possibly juvenile, the surface ornamentation is reduced to a single central occlusal crest with a few weakly marked cusps along it, and a single labial accessory cusp overlying a broad labial process. Such teeth are similar in shape to but broader than teeth of *Lonchidion breve* : they are particularly like *L. breve pustulatum* (Text-fig. 19), a subspecies known only from the *Perna* Bed at the base of the Atherfield Clay. The histological structure of the teeth of *Lonchidion breve*, with their very thick

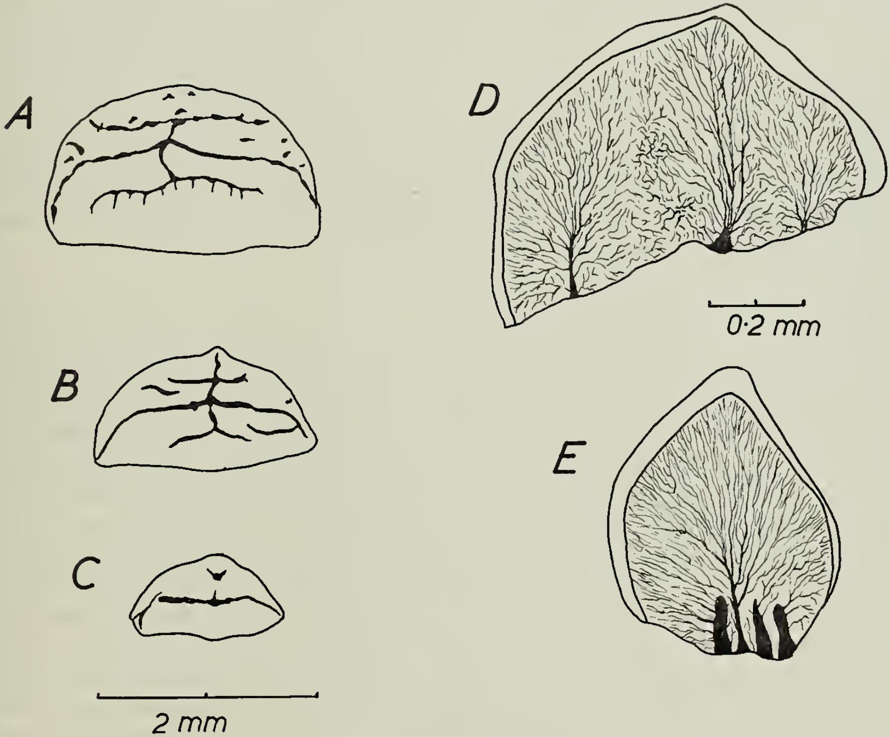


FIG. 29. A–C. Posterior teeth of *Hylaeobatis ornata* (Smith Woodward) from the Weald Clay of Henfield, Sussex, in occlusal view, to show the transition from normal posterior teeth (A) to (?) juvenile teeth (C) which resemble *Lonchidion*. P.47268–70. D. Transverse section of a small posterior tooth crown of *Hylaeobatis ornata*, P.47278, Weald Clay ; Henfield, Sussex. E. Transverse section of a tooth crown of *Lonchidion breve breve* sp. nov., P.47279, Ashdown Beds, Cliff End Bone-bed ; Cliff End, Sussex.

pallial dentine, seems at first to be against any relationship with *Hylaeobatis*, in which the crown consists mainly of osteodentine with a rather thin layer of pallial dentine whose tubules arise in bunches from the terminal parts of the vascular canals of the osteodentine (see p. 331 for discussion of Glikman's (1964) views on the differences between these types of tooth structure). But the differences here seem to be due largely to the greater size and thickness of the crown in *Hylaeobatis*. In *Lonchidion* the tubules of the pallial dentine arise from the tips of vascular canals, just as in *Hylaeobatis*, but the crown is so low and narrow that there is normally only a single row of vascular canals at the base of the crown : other vascular canals are sometimes present (Text-fig. 29E), from which a few short dentine tubules are given off into the basal parts of the crown. In the smallest teeth of *Hylaeobatis* (Text-fig. 29D) the structure may be very like that of *Lonchidion* : in these teeth the vascular canals only enter the base of the crown, there giving off sprays of pallial dentine tubules which make up the bulk of the crown. The type of structure seen in the teeth of *Hylaeobatis* can be derived from that of *Lonchidion* by increase in the breadth of the crown, making more vascular canals and tufts of pallial tubules necessary, and increase in the depth of the crown without increase in the thickness of the pallial dentine, allowing the basal part of the crown to be formed by osteodentine laid down around the vascular canals.

At present, I would suggest that *Hylaeobatis* (and the Ptychodontidae) arose from a homodont species of the hybodontid genus *Lonchidion*, primarily by reduction in the labial process, by increase in the surface ornament, by specialization in the anterior teeth, and by loss of fin and cephalic spines.

Relationships within the Ptychodontidae

The Ptychodontidae contains only the three genera *Ptychodus*, *Hylaeobatis* and *Heteroptychodus*. *Heteroptychodus* Yabe & Obata (1930 : 6), type species *H. steinmanni* Yabe & Obata (1930 : 7, pl. 2, figs. 6–8), is known only by a single tooth crown from the basal Cretaceous of Japan. This tooth is quite unlike *Hylaeobatis* and rather unlike *Ptychodus*, but the genus is so poorly known that nothing is to be gained from discussing it. I agree with Smith Woodward (1912 : 245) that the separate genus *Hemiptychodus* Jaekel (1894 : 137) for *P. mortoni* Mantell, in which the striae radiate from the centre of the tooth crown, is not justified.

Since *Hylaeobatis* is unknown above the base of the Aptian and *Ptychodus* does not appear until the Cenomanian there is a long gap in the history of the Ptychodontidae, and the two genera are not necessarily closely related. There is a number of characters in which *Ptychodus* is more specialized than *Hylaeobatis*, including :

1. Differences between the dentition of the two jaws in *Ptychodus*, one having very small symphysial teeth and large parasymphysials, the other having the largest teeth on the symphysis. Smith Woodward (1904), on the basis of a specimen in the Willett Collection in Brighton Museum in which the greater part of the cartilage of one jaw and fragments of the other are preserved, interpreted the jaw with the small symphysial teeth as the upper, but Canavari (1916 : 92) has shown that these small symphysial teeth were sunk beneath the level of the parasymphysials so that

they were not functional but formed the floor of a median groove in the dentition. He argues that such a groove would be without function in the upper jaw, but that in the lower it would serve as a gutter down which masticated food would be washed to the oesophagus. This interpretation seems reasonable and may provide an explanation for this difference between *Ptychodus* and *Hylaeobatis*, in which there is no evidence of differentiation between the upper and lower dentition.

2. Differences in the histological structure of the teeth. In *Ptychodus* (Owen 1840, pls. 18, 19; Casier 1953, pl. 1) the vascular canals of the crown are long, straight, and parallel through the greater part of their length, producing a tissue which resembles the tubular dentine of holocephalans and dipnoans. This type of tissue is an adaptation to a durophagous diet (Radinsky 1961 : 79) which has arisen independently in a number of groups, including rays, *Ptychodus* and *Asteracanthus* among selachians. The type of structure seen in *Ptychodus* can probably be derived from that in *Hylaeobatis* by alignment of the ascending vascular canals which give off the pallial dentine, in just the same way as the teeth of the hybodontid *Asteracanthus* (*Ptychodus*-like in structure) are probably derived from those of *Acrodus* (*Hylaeobatis*-like in structure).

3. *Ptychodus* is thought to have had calcified vertebral centra, while there is no evidence for such structures in *Hylaeobatis*. Direct evidence for the presence of calcified centra in *Ptychodus* rests on two specimens, one from the English Chalk (39436, *P. decurrens*; Smith Woodward 1912, pl. 52, figs. 1–6) in which two centra are preserved in association with fragments of calcified cartilage and twenty-three scattered teeth, and one from the Italian Upper Senonian, the holotype of *P. mediterraneus* Canavari (1916), in which an impression of a single centrum is preserved in association with an almost complete dentition. In my opinion there is still considerable doubt as to the weight to be attached to these specimens. In favour of the centra belonging to the same animal as the teeth is the fact that both the centra and the teeth in the two specimens are of approximately the same size (the centra *c.* 50 mm. in diameter in both, parasymphysial teeth from the lower jaw *c.* 35 × 29 mm. in Canavari's specimen, 34 × 31 mm. in the English specimen): it is unlikely that this should be so if the teeth and centra were associated either by chance or by the ingestion of *Ptychodus* by a shark with calcified centra. Against the centra belonging to *Ptychodus* there are several points. First, as Smith Woodward (1912 : 229) noted, the centra are very like those found in association with teeth of *Squalicorax* in the Kansas Chalk, where there is no doubt that the teeth and vertebrae are from the same animal: I have been unable to find any significant differences between the two types of centra in external or internal structure. Secondly, a considerable number of associated dentitions of *Ptychodus* has been collected in the English and American Chalk: it seems strange that only in one of these (one of the least complete) are centra preserved. Thirdly, calcified centra are not known in any other hybodontiform shark. It appears that there is not enough evidence to regard the presence of centra as a genuine difference between *Hylaeobatis* and *Ptychodus*.

The earliest well-known species of *Ptychodus* is *P. decurrens* Agassiz, the only species known in the Cenomanian zones of the English Chalk (Dibley 1911 : 273).

This species is more like *Hylaeobatis* than are later species in that there is no broad, flat, marginal zone on the crown, and it is therefore probably primitive. As the symphysial teeth of *Ptychodus* are the most specialized, one may expect that, as in *Hylaeobatis*, the small posterior teeth will show most resemblance to the ancestral form. A posterior tooth of *P. decurrens* is shown in Text-fig. 30A. Although larger and more strongly ornamented than posterior teeth of *Hylaeobatis*, it shows the same relative proportions of crown and root, and has an approximately similar surface

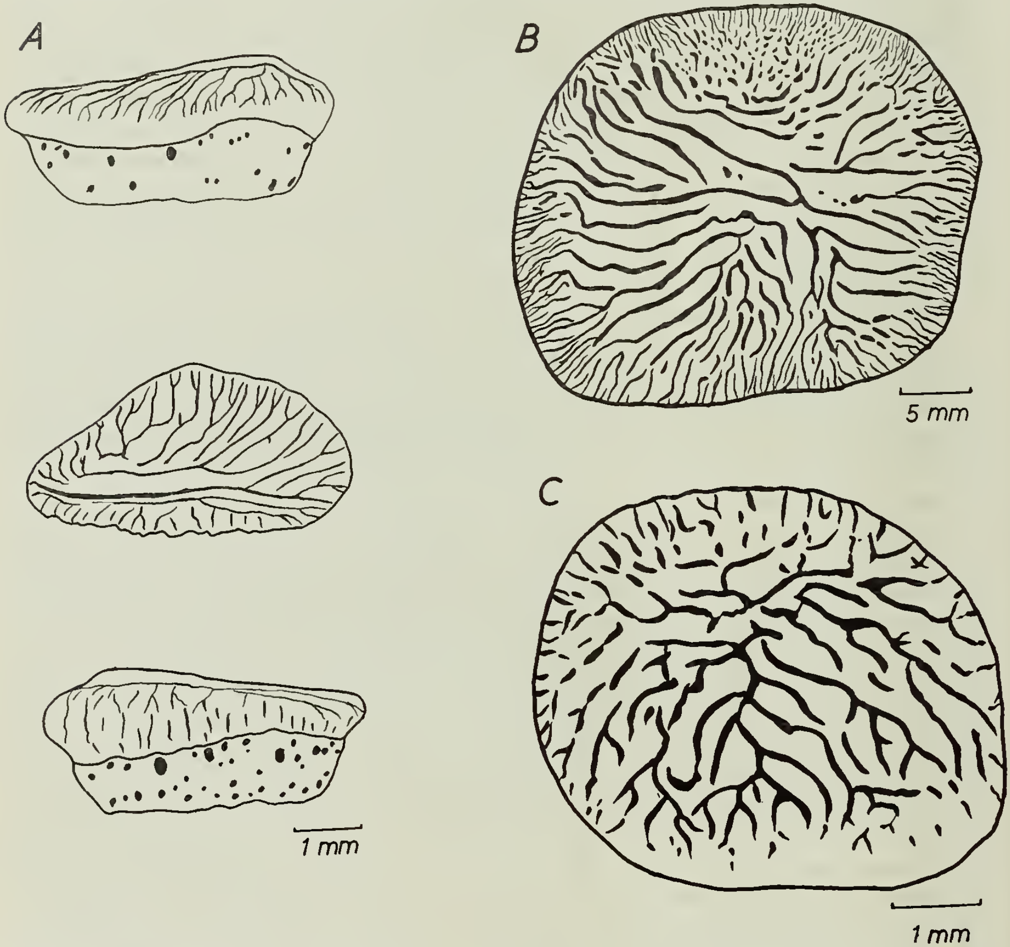


Fig. 30. A. *Ptychodus decurrens* Agassiz. Posterior tooth in labial (above), occlusal (centre) and lingual view. 4361, Lower Chalk; Lewes, Sussex. B. *Ptychodus decurrens* var. *oweni* Dixon. Parasymphysial tooth, probably from the first paired file of the upper jaw, right side, in occlusal view (symphysis to the right, labial margin uppermost). 39125, Lower Chalk; Halling, Kent. C. *Hylaeobatis ornata* (Smith Woodward). Antero-lateral tooth from the second paired file in occlusal view (symphysis to the left, labial margin uppermost). P.47230, Weald Clay; Henfield, Sussex.

ornamentation, a longitudinal occlusal crest from which bifurcating striae diverge. The arrangement of the striae tends towards the parallel ridges characteristic of anterior teeth in *Ptychodus*, but parallel transverse ridges also tend to develop in posterior teeth of *Hylaeobatis* (p. 337). Differences between teeth of *P. decurrens* and *Hylaeobatis* include :

1. The striae on the crown in *Ptychodus* extend almost to the root/crown junction on all surfaces of the tooth : this seems to be true of all except the smallest posterior teeth (Text-fig. 30A). In *Hylaeobatis* the lingual face of the crown is always smooth or nearly so, and on the other faces the striae end well above the root/crown junction.

2. In *Hylaeobatis* the whole of the lingual face of the crown is occupied by a concavity in which the labial surface of the succeeding tooth fits : this is true even of the smallest teeth. In the small posterior teeth of *Ptychodus* there may be no cavity at all, as in Text-fig. 30A, while in the anterior teeth the cavity is always rather small and often appears to be more a pressure scar caused by the succeeding tooth rather than a real feature of the tooth. In *Ptychodus* the surface of the lingual cavity is always ornamented, like the rest of the crown, while in *Hylaeobatis* it is smooth. This seems to imply that in *Ptychodus* the fit between successive teeth was not so close as it was in *Hylaeobatis*.

3. In *Ptychodus* the crowns of the anterior teeth are almost square or only slightly longer than broad. There is no counterpart in *Ptychodus* of the transversely elongated symphysial and parasymphysial teeth of *Hylaeobatis*, nor is there any sign in *Ptychodus* of the labial shifting of the main occlusal crest which is characteristic of these anterior teeth in *Hylaeobatis*. But the antero-lateral teeth of *Hylaeobatis* (II, Text-fig. 28) are almost identical in shape with parasymphysial teeth of *P. decurrens*, and in the ornamentation of the crown they are very close to *P. decurrens* var. *oweni* (Smith Woodward 1912, pl. 52, figs. 9–11) a form in which the striae are more irregular than they are in typical examples of the species. The teeth shown in Text-fig. 30B, C demonstrate this very close similarity, the only difference between the two being the finer and more extensive ornamentation of *P. decurrens*, a feature which could well be due simply to the much larger size of the latter.

In summary, there are some characters in which *Ptychodus* is more advanced than *Hylaeobatis*, particularly the histological structure of the teeth and the different form of the symphysial teeth in the upper and lower jaws, but both these characters could have evolved from the conditions in *Hylaeobatis*. In *Ptychodus* the crown is more heavily and extensively ornamented than in *Hylaeobatis*, and there was a less close fit between successive teeth—in the first of these characters *Ptychodus* is probably more advanced than *Hylaeobatis*, in the second more generalized, but again these conditions could be derived from those in *Hylaeobatis*. In *Ptychodus* there is no counterpart of the specialized elongated symphysial and parasymphysial teeth of *Hylaeobatis*, but there is a close similarity between the antero-lateral teeth of the second paired file in *Hylaeobatis* and the parasymphysial teeth of *P. decurrens*. This suggests that *Ptychodus* did not evolve direct from *Hylaeobatis*, or at least not from the only known species of that genus, but from a similar form in which the symphysial and parasymphysial teeth were less specialized.

IV ECOLOGY AND RELATIONSHIPS OF THE FAUNA

It now seems certain that the bulk of British Wealden (excepting the upper part of the Weald Clay and the Wealden Shales: Anderson 1963; Casey 1961 : 490) and the greater part of the Middle and Upper Purbeck (Anderson 1958) were laid down in fresh water (Allen 1959). At Henfield this is confirmed for the fish horizons by the ostracods and charophytes (see p. 286). The abundance and variety of the shark fauna is therefore surprising, for shark remains are normally taken as evidence of marine or estuarine conditions, since among living elasmobranchs only some species of *Carcharhinus*, potamotrygonid rays and pristids have become adapted to life in fresh or brackish water. As for the hybodonts, Casier (1961 : 77) is of the opinion that they were all marine while Estes (1964 : 167) notes that *Lonchidion selachos* is only the second freshwater form known, the other being *Lissodus africanus* (Brough 1935). It is notable that none of the more advanced selachian groups is present in the British Wealden and Purbeck, although notidanids, heterodontids, orectolobids scyliorhinids, squalids, squatinids and rhinobatids were already present in Upper Jurassic seas: this provides additional evidence that the deposits were laid down in fresh water. The moderately large and varied hybodont fauna of the English Wealden and Purbeck shows that by the end of the Jurassic (if not before) some hybodont sharks had become euryhaline and entered fresh waters. This move was clearly advantageous: it removed the hybodonts from competition with more advanced forms, some of which (particularly notidanids, heterodontids, orectolobids, rhinobatids) must have occupied very similar niches, and allowed them free rein as almost the only aquatic predators among the rich teleostean, molluscan and arthropodan fauna of the Wealden lakes and rivers. The hybodonts were here able to undergo a new adaptive radiation, analogous to their marine radiation at their first appearance in the Triassic. This radiation, taking place in the absence of other selachian competitors, is almost certainly responsible for the similarity between the Cretaceous freshwater selachian fauna and the Triassic marine fauna which emerges from a list of the species most resembling the Wealden forms. The high-crowned Wealden *Hybodus* species, *H. basanus*, *H. ensis* and *H. parvidens*, resemble similar forms which occur throughout the Triassic and Jurassic. The low-crowned *H. brevicostatus* is most like the larger Triassic *Polyacrodus* species and low-crowned Liassic *Hybodus* such as *H. delabechei*. *Lonchidion breve* resembles the Triassic *Lissodus* and Triassic teeth assigned to *Palaeobates*; *L. striatum* resembles the smaller Triassic *Polyacrodus* species; *L. heterodon* is another form resembling Triassic *Palaeobates*. *Lonchidion rhizion* and *Hylaeobatis* are the only entirely novel forms in the Wealden, the first apparently unique, the second leading on to the Upper Cretaceous ptychodonts. Other specialized Lower Cretaceous hybodonts include the ' hybodontoïde de position systematique indeterminée ' described by Casier (1961 : 18, pl. 3, figs. 3–6, text-figs. 2, 3) from the Congo, in which there is a very deep root with two large canals in the centre and a low, crescentic crown of *Acrodus*-like histological structure. This form, known by isolated teeth from a number of localities, is quite possibly another freshwater hybodont. It occurs in

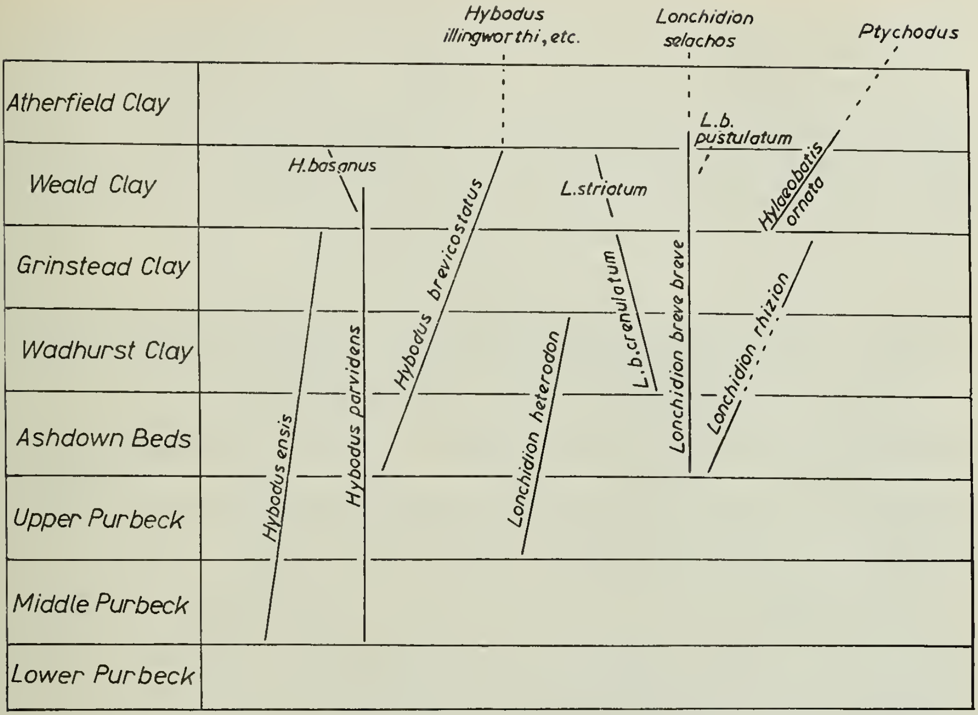


FIG. 31. Diagram showing the probable interrelationships of the sharks of the British Wealden and Purbeck and certain Upper Cretaceous species. Lines converging upwards indicate convergent evolution, lines converging downwards indicate phylogenetic relationship. Only those formations from which sharks are known are included.

beds of freshwater character (Casier 1961 : 73) which Casier finds to be marine largely because *Hybodus*, which he thought to be exclusively marine, is present (p. 77).

It seems probable that the hybodonts successful invasion of fresh water in the Lower Cretaceous was not permanent : some euryhalinity was retained, and in the Upper Wealden some of the more specialized forms were able not only to accommodate to the influx of salt water at the end of the Wealden, but to compete successfully with the more advanced selachians present in the sea. The last of the marine hybodontids (*Hybodus illingworthi*, *Acrodus dolloi*, etc., Cenomanian to Senonian) are probably derived from the Wealden *H. brevicostatus*, and the ptychodonts, highly successful and widely distributed in the Upper Cretaceous, seem to have evolved from near the Wealden *Hylaeobatis*.

Within the Wealden and Purbeck, fairly large samples of teeth from successive horizons give an unusually complete and well documented account of the evolution of the various species. These changes are summarized in Text-fig. 31, the details being given in the descriptions of the species. I have no doubt that this diagram is a gross simplification of the true picture, and that further sampling will produce additions to the fauna and to the complexity of the dendrogram.

This work has been made possible by those who have collected and presented the bulk of the new material described : Dr. K. A. Kermack and his colleagues at University College and Messrs J. F. Wyley, I. M. West, P. J. Whybrow and B. H. Newman. I am most grateful to all these gentlemen, in particular to Mr. Wyley for his careful collecting at Henfield and for allowing me to accompany him on visits to the pit. My thanks are also due to Dr. F. W. Anderson of H.M. Geological Survey, who has kindly examined samples of ostracods from Henfield, to Mr. H. A. Toombs for his help, and to Mr. P. J. Green, who took the photographs.

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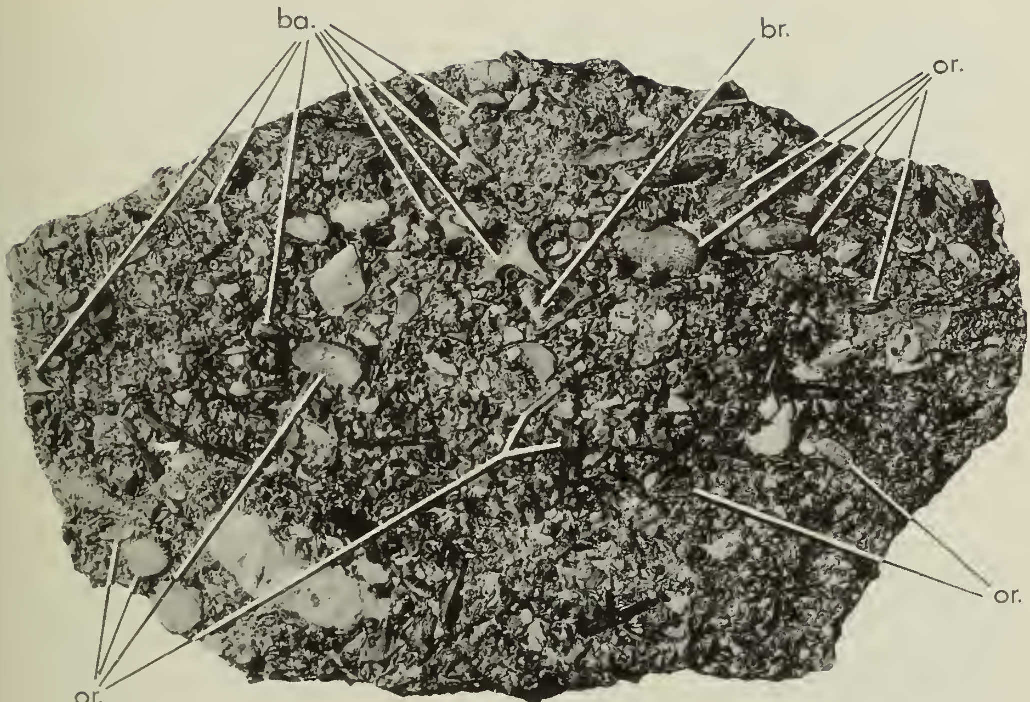
PLATE 1

FIG. 1. A block of bone-bed from the Weald Clay, Henfield Brick Co. pit, Henfield, Sussex. Teeth of *Hybodus basanus*, *H. brevicostatus* and *Hylaeobatis ornata* are indicated by 'ba.', 'br.' and 'or.' respectively. P.46920. ×1·5.

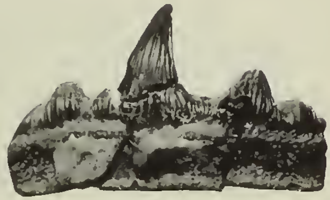
FIG. 2. *Caturus tenuidens* Smith Woodward. A fragment of right dentary in lateral view. Weald Clay; Henfield, Sussex. P.46837. ×4.

FIG. 3. *Hybodus brevicostatus* sp. nov. Upper anterior tooth in labial (*a*) and lingual (*b*) view. Wadhurst Clay; Hastings, Sussex. P.11876. ×3.

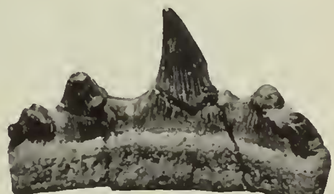


1

2



3a



3b

PLATE 2

Hybodus brevicostatus sp. nov.

Teeth of the holotype, P.46973, Weald Clay ; Henfield, Sussex. All $\times 4$.

FIG. 1. Upper symphysial tooth in labial (*a*) and lingual (*b*) view.
FIG. 2. Tooth from the fifth file of the right upper jaw in labial (*a*) and occlusal (*b*) view.
FIG. 3. Tooth from the first file of the left lower jaw in labial (*a*) and occlusal (*b*) view.
FIG. 4. Tooth from the sixth file of the left lower jaw in labial (*a*) and lingual (*b*) view.
FIG. 5. Tooth from the eighth file of the left lower jaw in labial (*a*) and occlusal (*b*) view.
FIG. 6. Tooth from the ninth file of the left upper jaw in labial (*a*) and lingual (*b*) view.

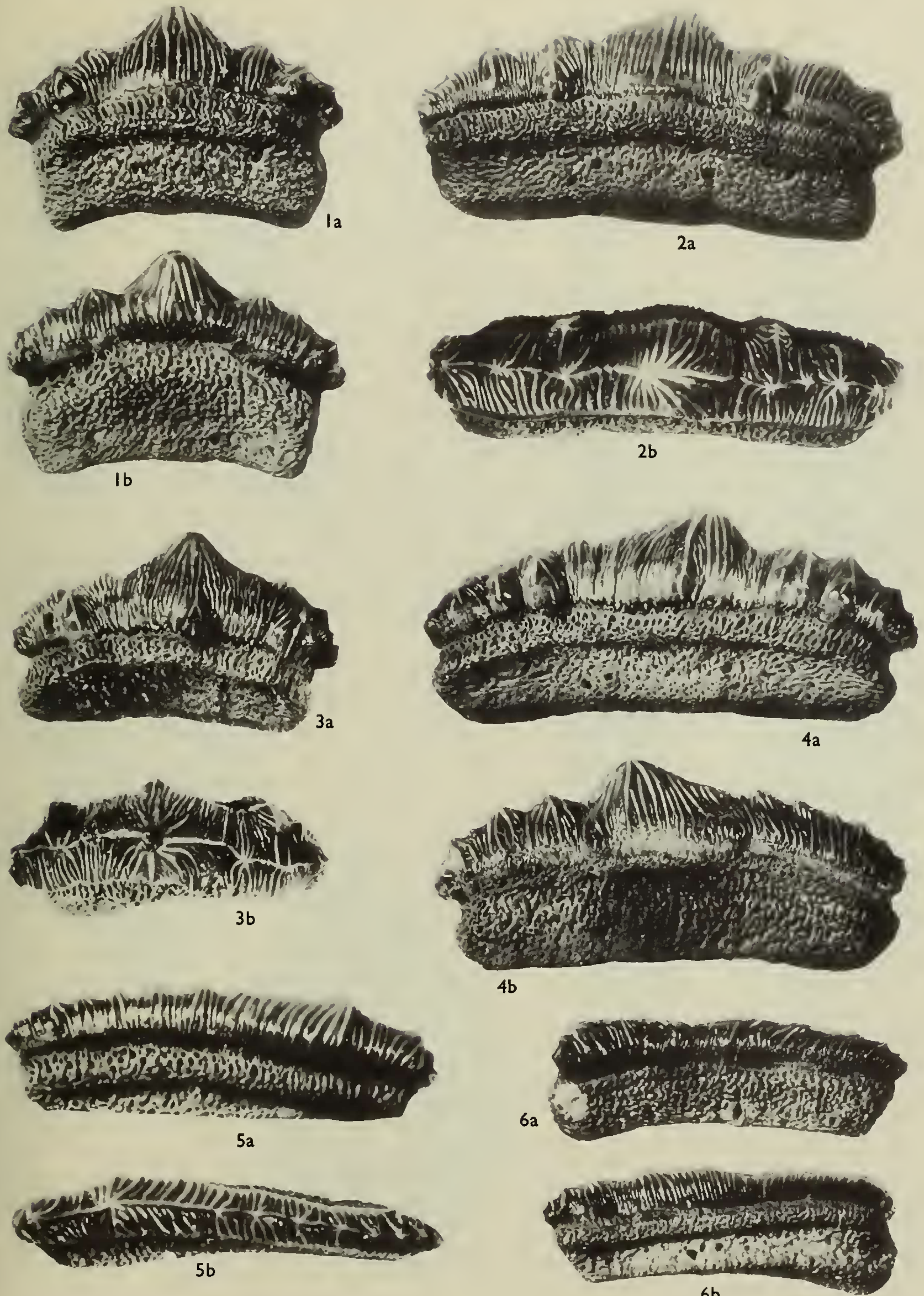

1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b

PLATE 3

Figs. 1, 2. *Hybodus brevicostatus* sp. nov. Dorsal fin spines in posterior (*a*) and right lateral (*b*) view, natural size, with outline sections ($\times 1{\cdot}5$) at the points marked. Fig. 1, the holotype, P.46973, Weald Clay; Henfield, Sussex. Fig. 2, P. 13268, Wealden Shales (overlying *Hypsilophodon* Bed); Cowleaze Chine, Isle of Wight.

Fig. 3. *Hybodus brevicostatus* sp. nov. Thin section of a tooth from the holotype, P. 46973, Weald Clay; Henfield, Sussex. $\times 12$.

Fig. 4. *Lonchidion* sp. Thin section of a dorsal fin spine, cut at the level marked in Text-fig. 26A. P.47208, Weald Clay; Henfield, Sussex. $\times 12$.

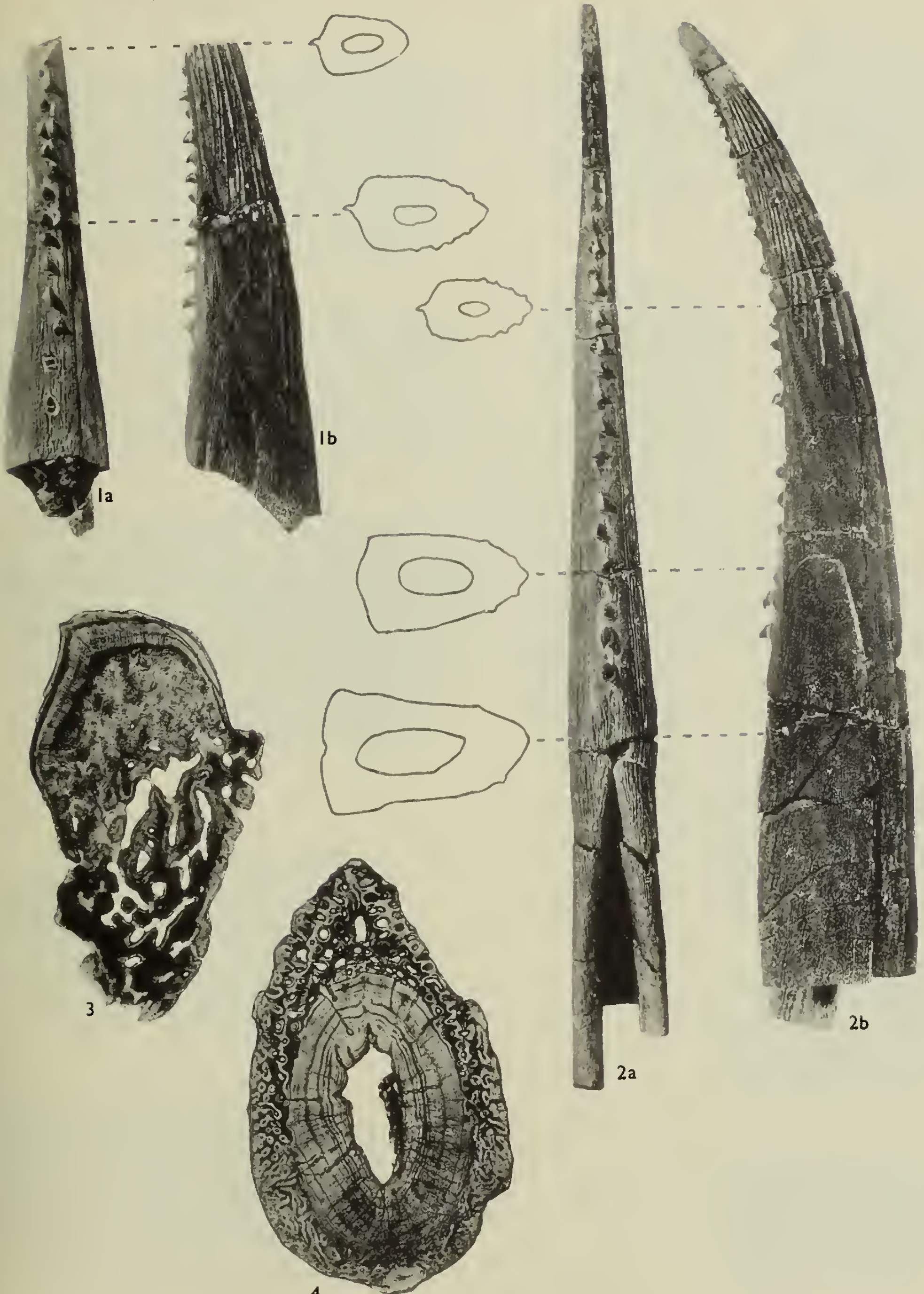

1a
1b
2a
2b
3
4

PLATE 4

Hylaeobatis ornata (Smith Woodward)

Teeth from the Weald Clay of Henfield, Sussex. ×5.

FIG. 1. Symphysial tooth in labial (*a*), occlusal (*b*), lingual (*c*) and lateral (*d*) view. P.47211.

FIG. 2. Parasymphysial (first paired file) tooth in labial (*a*) and lingual (*b*) view. P.47212.

FIG. 3. Antero-lateral (second paired file) tooth in labial (*a*), occlusal (*b*), lingual (*c*) and lateral (*d*) view. P.47213.

FIG. 4. Lateral tooth (probably fourth paired file) in labial (*a*), occlusal (*b*) and lingual (*c*) view. P.47214.

PLATE 4

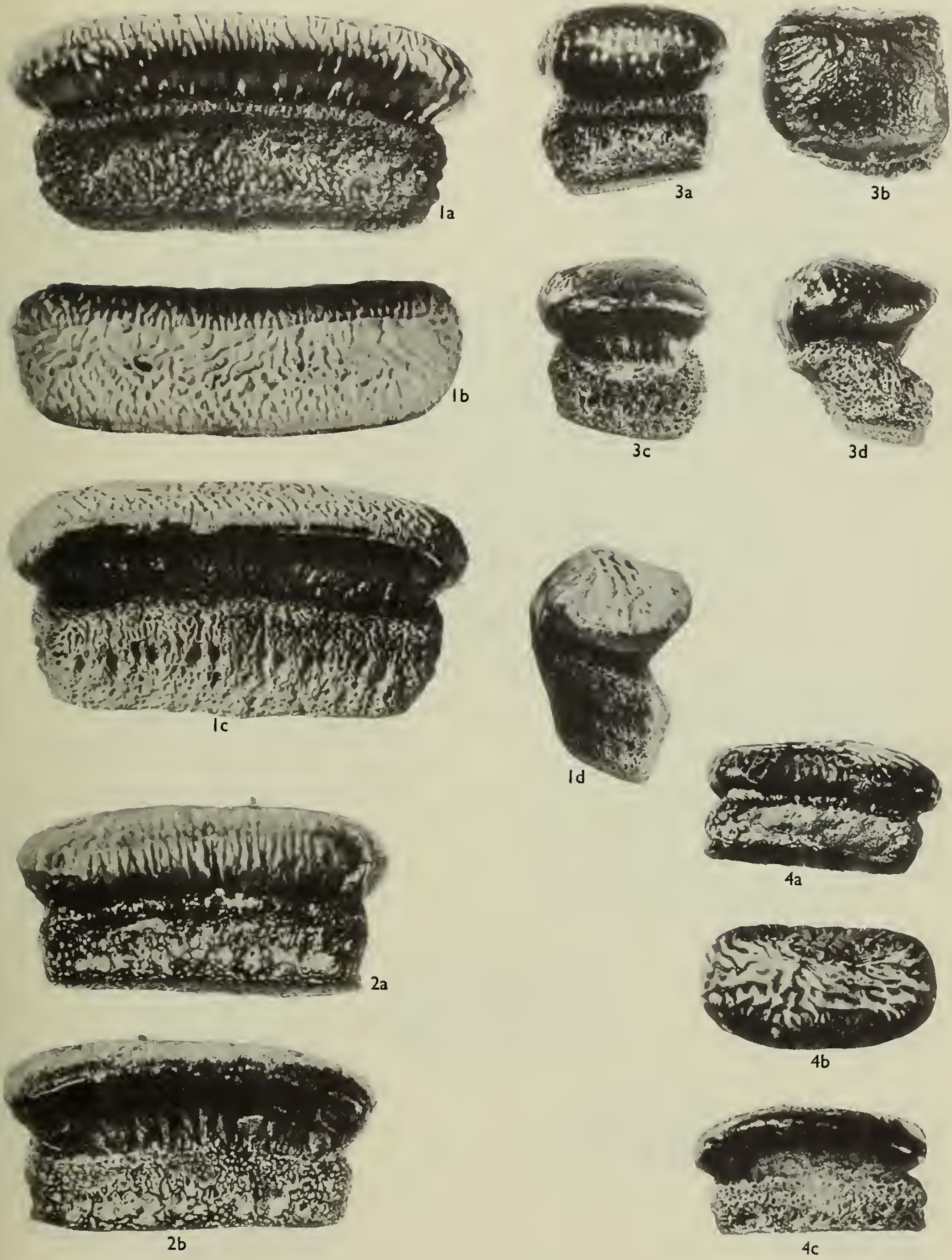


PLATE 5

FIG. 1. *Polyacrodus minimus* (Agassiz). Vertical section of tooth crown. P.47271, Rhaetic; Holwell, Frome, Somerset. ×30.

FIG. 2. *Palaeobates angustissimus* (Agassiz). Vertical section of tooth, P.47272, Muschelkalk; Crailsheim, Germany. ×20.

FIG. 3. *Lonchidion breve breve* sp. & ssp. nov. Vertical section of tooth crown cut through the labial process. P.47275, Ashdown Beds, Cliff End bone-bed; Cliff End, Sussex. ×50.

FIGS. 4, 5. *Hylaeobatis ornata* (Smith Woodward). Vertical sections of crowns of a parasymphysial tooth (Fig. 4, P.47276, ×20) and a posterior tooth (Fig. 5, P.47277, ×40), Weald Clay; Henfield, Sussex.

FIGS. 6, 7. *Hylaeobatis ornata* (Smith Woodward). Teeth in labial (*a*), occlusal (*b*) and lingual (*c*) view, Weald Clay; Henfield, Sussex. Fig. 6. Posterior tooth (probably eighth paired file), P.47216, ×10. Fig. 7. Postero-lateral tooth (probably sixth paired file), P.47215, ×5.


1
2
3
4
5
6a
6b
6c
7a
7b
7c